

**An ecological and molecular study of the European
nightjar (*Caprimulgus europaeus*) and its allies**

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AN ECOLOGICAL AND MOLECULAR STUDY OF THE EUROPEAN NIGHTJAR, (CAPRIMULGUS EUROPAEUS) AND ITS ALLIES

Abstract

This thesis covers two broad areas of investigation; the conservation ecology of the European nightjar (*Caprimulgus europaeus*) nesting in lowland pine plantations in Eastern and Southern England and the application of phylogenetic methods to the Caprimulgidae. The nightjar has become a popular study organism with many studies involving the use of mist netting and attachment of GPS tags. However the effects of such close contact and potentially high degree of disturbance has not been studied systematically. The ecological work aimed to determine the effects of capture, instrumentation and blood sampling on breeding nightjars and also habitat selection for nesting and the importance of disturbance induced predation using artificial nests. Mist netting, telemetry and blood sampling had no effect on breeding success and no measurable long terms effects on philopatry or survival. Mist netting resulted in 0.75% mortality. Radio tagging caused short term reduction in activity and minor feather wear. Blood sampling caused temporary weight loss in bled chicks. We recommend that feathers are used instead of blood for DNA analysis. Telemetry showed that song territories (territory used primarily for nesting) of mated and unmated males were similar and nightjars shared airspace above territories so census workers should factor this into surveys. Male nightjars established territories on clearfell, plantations less than 10 years old and heathland but avoided plantations when the canopy has closed. Territory size varied by habitat (mean range 4.6ha to 9.3ha) but all territories had a compactness ratio (circularity) greater than 0.64 (where 1 = perfect circle). Nightjars located their nests adjacent to soft edges (broad transition of vegetation of similar height) and chose vegetation of intermediate density requiring a balance between nest concealment and vigilance. Artificial nests were created on habitat used by nightjars and baited with quail and plasticine eggs. Depredation was similar to nightjar nests however predation of nightjar and quail nests was mainly avian, whereas plasticine eggs were predated by mammals. These findings recommend future studies should avoid using plasticine eggs and use cameras to record predation events. Depredation was higher on clearfells and lowest in 4-9 year plantations and heathlands. Success of artificial nests on bracken dominated clearfells and <4 year plantations increased when visited. Depredation was higher and more rapid in large territories and when adjacent to hard edges but lower and less rapid with higher vegetation density and territory compactness. The implications of this study are that controlled disturbance does not increase nest predation but that both real and artificial nest survival is dependent on optimal vegetation cover. These results have important implications for habitat conservation initiatives for this species nesting in commercial pine plantations. In the phylogeny work, cytochrome *b* was used as a probe. Bayesian analysis found that within the *Caprimulgidae* there were four geographically isolated clades with bootstrap support greater than 70%. Phylogeny

suggests that the genus *Caprimulgus* is not monophyletic and is restricted to Africa and Eurasia and that *Caprimulgus* species from outside this area have been misclassified as a consequence of retention of primitive adaptations for crepuscular/nocturnal living. Future studies should use a more slowly evolving gene and include more taxa. The phylogeny was used to investigate the ecological correlates of bristle variation. Functional bristles were absent in the majority of the nighthawks and varied in the remaining two New World nightjar radiations and the Old World radiation. The length, number and stiffness of facial bristles on museum specimens of the Caprimulgiformes were measured. A phylogenetically controlled comparative analysis suggested that rictal bristles have a mechanical role in protecting delicate head structures in general (habitat used for nesting) and foraging habitats. Complex foraging habitats selected for longer, more flexible rictal bristles that might have improved mechanoreception while such bristles were shorter in semi-open foraging habitats and vestigial in open habitats. Bristles are primitive and have become vestigial multiple times within this Order. These events are associated with habitat shifts leading to changes in foraging behaviour and selection on bristle characteristics, which in turn may have led to speciation.

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CHAPTER ONE

AN INTRODUCTION TO NIGHTJAR CONSERVATION ECOLOGY, TAXONOMY AND PHYLOGENETIC COMPARATIVE METHOD.

1.1 INTRODUCTION

1.1.1. Applied ecology and bird conservation

In keeping with the philosophy of other studies on threatened and poorly studied species this part of the thesis aims to provide a detailed evidence based understanding of the habitat use and behavioural responses to disturbance of one of the UK's most enigmatic species, the European nightjar, (*Caprimulgus europaeus*) (hereafter nightjar) nesting in lowland pine plantations, with a view to informing conservation management efforts. At the time of completion of the fieldwork between 1994 and 1998 little work had been published on habitat selection for song territories in nightjars (Bowden and Green 1991) and even less on home range analysis (Alexander and Cresswell 1990). However, the nightjar has become a 'desirable' study organism and the publication of a number of studies since early 2000 have meant that much of this early work has lost its scientific impact. Consequently, two studies that were intended for inclusion in this thesis, one focussing on habitat use versus availability for home range and analysis of foraging activity in relation to breeding cycle and foraging habitat quality, are not included in this thesis. Instead, the focus of the remaining ecological work addresses questions about habitat selection in relation to predator avoidance and the consequence of disturbance for nest predation.

Such depth of knowledge is increasingly recognised as important to the success of conservation initiatives (Dicks *et al.* 2013) and especially so for critically endangered species (Pople 2003). Knowledge of habitat use provides habitat managers with an understanding of preference relative to availability, habitat utilisation for nesting, roosting and foraging and susceptibility to disturbance and predation (e.g., Brown 1988). Such knowledge allows conservationists to apply a hierarchical evaluation of habitat

importance to the focal organism and therein prioritise resource allocation (e.g., Jones 2001). For example, Harris *et al.* (2008) investigated the habitat preferences of African elephants (*Loxodonta africana*) in 3 reserves in southern Africa. Conservationists were concerned by the environmental degradation caused by the growing elephant population and sought alternative management to culling and relocation. They found that proximity of water was the most important determinant of habitat occupancy, followed by presence of vegetation (for food and cover) and finally absence of human settlements.

A detailed understanding of habitat use for different activities might reveal the sensitivity of birds to disturbance at different spatial and temporal scales. For example, land modification and land use change including the creation of 'hard edges' (vegetation of contrasting height) has a more significant effect on birds during the breeding season (Angelstam 1986, Yahner 1988, Ries *et al.* 2004, Suvorov, Svobodová and Albrecht 2014) and have been shown to disproportionately affect species susceptible to disturbance (Reino *et al.* 2009). The incidence of nest predation and parasitism is considerably higher near edges and open nest species on the ground might be particularly vulnerable to land disturbance and the creation of 'hard edges' (Yahner 1988, Suvorov, Svobodová, Koubová, and Dohnalová 2012). Other potential threats to ground nesting birds include recreation pressure (Mallord *et al.* 2007) and research activity (Ibáñez-Álamo, Sanllorente, and Soler 2011).

Foraging animals might be particularly sensitive to disturbance in very open habitats intensively used by humans (e.g., piping plovers (*Charadrius melodus*) feeding on coastal habitats, Burger 1994) or at 'natural' feeding sites during migration (e.g., snow geese (*Chen caerulescens*) (Bechet *et al.* 2004). Understanding the foraging habits of focal species is also critical to successful habitat management. Studies of this nature can be used to: understand predator behaviour and how this shapes community structure (Heithaus *et al.* 2008); enhance the reproductive success and population diversity of species through supplementary feeding, e.g., hummingbirds, (*Saliva mexicana* and *S.*

fulgens) in regions near nectar feeders (del Coro Arizmendi *et al.* 2008) and, provide additional food sources for declining species, e.g., turtle dove (*Streptopelia turtu*), UK (Browne and Aebischer, 2003). By focusing on dietary requirements researchers can reveal inter and intraspecific competition amongst species (e.g., Poling and Hayslette 2006) and make inferences about the carrying capacity of the habitat (Tamaki *et al.* 2008).

1.1.2. Forest management

Enhancement of biodiversity has become an important goal of forest management (Lawton *et al.* 2010, Lindenmayer, Margules and Botkin 2001). However, bird conservation can be challenging in landscapes with high habitat turnover (such as coniferous plantations), due to clearfelling and rapid succession, especially for species that require mosaics of early successional habitat for nesting and deciduous woodland patches and matrices of conifer plantation for foraging (e.g., Barbaro *et al.* 2007). One such management technique is the establishment and maintenance of open habitat to increase vegetation heterogeneity and ultimately species diversity (Forestry Commission 2004). For example, hoverfly diversity increased in tandem with glade and ride creation in Irish conifer plantations (Gittings *et al.* 2006) and vascular plant diversity increased in rides and glades within 1 km of native woodland in another conifer plantation in Ireland (Smith *et al.* 2007). Indeed, Lepidoptera species associated with woodland also require open habitat for foraging, basking and/or egg-laying (e.g., white admiral (*Limenitis camilla*) and pearl bordered fritillary (*Boloria euphrosyne*), Clark *et al.* 2011). In the UK, the Open Habitat Policy of the Forestry Commission has been developed to create diverse landscapes of forest and open habitat, replacing forest with important and threatened open habitats such as heathland and marshland (Driver 2010). Such habitats are often associated with species of conservation concern requiring open matrices within forest habitats and include the nightjar, woodlark (*Lullula arborea*) and Dartford warbler (*Sylvia undata*).

1.1.3. The nightjar

The nightjar is a medium-sized (25-27.5cm – from bill tip to tail), sexually dimorphic member of the order Caprimulgiformes. At rest the species exhibits a cryptic colouration and plumage for background matching, typical of most nocturnal bird species (Figure 1.0). Due to their crepuscular and nocturnal habits, and propensity to nest and roost on the ground, the chromatic plumage of nightjars is highly conserved across genera and is cryptic consisting of largely melanin based pigments producing black, brown, beige, buff and chestnut feathers arranged in three broad plumage categories (Cleere 2010). This plumage results in 'general colour resemblance' often combined with disruptive colouration. Chicks also vary in their camouflage but in general they seem to adopt a masquerade camouflage (Skelhorn *et al.* 2010) by resembling natural features in their habitat such as fallen pine cones or pieces of tree bark (Figure 1.1). In flight the wings are fairly pointed and are reminiscent of a raptorial bird such as a small falcon. Flight is buoyant and rapid. Nightjars are capable of a slow gliding flight holding their wings in a stiff, deep V above the body. Due to their long wings and tail they are agile and can even sustain short periods of hovering. The male has a white spot on the three (but occasionally four) outer primaries and white tips to the two outer rectrices (tail feathers). Although females lack such white spots, older individuals (c4 years old) possess pale buff spots instead. The tarsi are rather short hence the bird shuffles when on the ground.



Figure 1.0 Male nightjar at daytime roost (Sherwood Pines Forest Park, Nottinghamshire)



Figure 1.1. One day old nightjar chick at nest with unhatched egg.

The following sections 1.1.3.i to 1.1.3.iii detail literature that is relevant to the ecological and behavioural chapters in this thesis. They provide details on the status, habitat requirements and territorial and breeding ecology of nightjars nesting in Europe and thus the context for these chapters in the thesis.

1.1.3.i. Status

The nightjar occurs right across the Palearctic ranging from north-western Europe through to central Asia, China and the Near East down into north-west Africa. The nominate race of the nightjar *C. e. europaeus* is the only caprimulgiform that breeds in the UK. It also breeds across much of Europe with an estimated population between 295,000 and 809,000 breeding pairs (Hagemeijer and Blair 1997). The race *C. e. meridionales* breeds in the southern and eastern regions of Europe (Cramp 1985). Four other races have been identified and include *C. e. sarudnyi*, *C. e. unwini*, *C. e. plumipes* and *C. e. dementievi* (Cleere, 1998). However, there is much clinal variation and intergradation. For example, *C. e. europaeus* becomes smaller southwards and smaller and greyer in the east of its range (Cramp 1985).

It is a summer migrant to Europe wintering in sub-Saharan Africa, and to a lesser extent in north-western India and Pakistan, migrating in small flocks (Cramp 1985). Males arrive on their UK breeding grounds from the first week of May in the south (pers. comm. Cresswell) of the country and as late as the beginning of June for the northern populations. Females tend to arrive about ten days after the males (Cleere 1998).

Approximately 50% of the breeding nightjar population is in Europe but here, it has experienced a rapid and widespread reduction in both range and numbers since the early 1950's (Hagemeijer and Blair 1997, Langston *et al.* 2007b). The decline in north-western Europe has been extreme. In the Netherlands for example, nightjars have suffered a 90% decrease since the 1950s with only 450-650 breeding pairs in 1992 largely attributed to habitat loss and fragmentation (Dijk *et al.* 1994). Consequently, the nightjar is a Species of

European Conservation Concern (SPEC 2) (Burfield and Van Bommel 2004) and is protected under the EC Habitat and Species directive (EC 1992). A survey in 1992 of the UK population, conducted by Morris *et al.* (1994), showed that numbers of singing males had risen in most counties from 2,100 recorded by Gribble in 1983, to over 3,400 (Morris *et al.* 1994). However, they concluded that the current population is less than 50% of that of the early 1970's, (see also Leslie, 1993). Accompanying the pre-1992 decline was a north and west contraction of range (Stafford, 1962; Gribble, 1983) and the nightjar was a red-listed species due to a decline of >50% in breeding range between 1972 and 1992 (Gregory *et al.* 2002).

Despite the general decline in Central England, North West England, Ireland and Scotland, which have largely been attributed to habitat loss and cropping patterns of forestry land, localised increases have occurred (Balmer *et al.* 2013). For example, in Wales, (Conway *et al.* 2007) and the north Yorkshire Moors (Scott *et al.* 1998) nightjars appear to be making an altitudinal shift to moorland and in the Dukeries of Nottinghamshire where they were declining but recent figures are promising (Conway *et al.* 2007). Southern England has also witnessed population growth within suitable habitat associated with sensitive heathland and forest management, as well as North East England and Eastern Scotland (Balmer *et al.* 2013). Although the 'preferred' breeding habitat of nightjars is heathland, nightjars in the UK are increasingly reliant on clear-felled and recently planted commercial forest (Morris *et al.* 1994; Conway *et al.* 2007). Researchers in Dorset (SRG 1994) have demonstrated an east to west movement in birds (especially adult males) caught and rung in previous years showing lateral movement between adjacent sites. However, some of these increases are now in reverse, and most notably in East Anglia which supports c10% of the UK population, and the population overall is fragmented and relictual (Conway *et al.* 2007; Conway and Henderson 2010). Through its partial recovery of UK range, nightjar moved from red-listed to amber in the latest review (Eaton *et al.* 2015).

Despite the increases in suitable habitat afforded by large scale felling of pines, ecologically aware changes in forest management and heathland improvement/restoration projects it is likely that there may be other factors inhibiting colonisation by nightjars. These range from reduced reproductive success attributed to climatic change and a consequent contraction of the breeding season and decline in large invertebrate prey, (Kemp, 1983; Berry & Bibby 1981) to recreational disturbance (Liley and Clarke 2003). Climatic change may have had a marked effect on the isolated populations in the north and west, especially as these tend to be in upland areas with typically high rainfall. Wetter summers with untypical late ground frosts may have had a two-fold effect. Firstly, ground frosts may delay egg-laying and shorten the breeding season (Berry 1979; Berry & Bibby 1981; Crick 2004) making second broods less likely. Secondly, colder wetter weather may reduce insect prey and thus compromise the birds' ability to raise a first brood (but see Cross *et al.* 2005). Personal observations suggest that wet and windy evenings inhibit moth activity and foraging. A further possible explanation for lack of population recovery is recreational disturbance. Causes of decline in the Midlands are attributed to recreational pressure (pers. comm. Gribble). Liley and Clarke (2003) found lower breeding densities on heathland adjacent to urban developments and nightjar (but found little evidence for increased predation) and breeding success was found to be lower with close proximity to recreational footpaths due to suspected avian predation when adults are flushed from the nest (Langston *et al.* 2007; Lowe, Rogers and Durrant 2014).

1.1.3. ii. Ecology and habitat requirements

Possibly because of its nocturnal behaviour and secretive breeding habits, at the time of writing, studies of the nightjar were limited both in number and scope. The majority of the research was restricted to studies regarding its breeding biology (Berry 1979, Berry & Bibby 1981) or habitat selection for breeding (Stafford 1962, Berry 1979, Hughes 1980) or foraging behaviour (Alexander and Cresswell 1990). Other studies have focused on the conservation and management of its habitat (Ravenscroft 1988, Burgess *et al.* 1989, Bowden & Green 1991). These studies showed that nightjars in the UK had made a habitat

shift from heathland to heathland/pine mosaics and preferred plantations less than 5 years old. From a habitat management perspective the study by Burgess *et al.* (1989) conducted on heathland in Suffolk is the most pertinent to nightjar conservation. The cumulative effect of the management was to increase the nightjar population from 5 churring males in 1978 (when the management began) to 23 in 1989. The bulk of the increase was directly attributable to the increased amount of edge habitat used by nightjars when foraging, although there was a general population increase during the study period in the region and throughout the UK (Morris *et al.* 1994). For example, in East Anglia the number of singing male nightjars rose by 94% from 301 (at 148 sites) to 585 (at 199 sites). In the UK in general the population increase was 74% (Morris *et al.* 1994). However, the nightjar population at Minsmere was not promoted above that predicted from changes in the woodland edge, thus the lack of nest sites may not have been limiting the population size before management was initiated. The only established benefit of increasing availability of potential nest-sites occurred in heavily predated areas, where nightjar fledgling success increased (Burgess *et al.* 1989).

Other work of note includes the study conducted by the Royal Society for the Protection of Birds on nightjars nesting on pine plantations in Norfolk. In this study Bowden and Green (1991) assessed the habitat requirements of nightjars during the breeding season and related these to forestry practice. They used VHF radio tracking technology to monitor habitat use so their findings are particularly relevant to the data presented in Chapter 3 and require a sufficiently detailed outline here.

They found that nightjar numbers had increased substantially in line with an increase in the area of young pine plantings. They also found that churring and displaying nightjars are most abundant on young plantations and nightjar density declined with plantation age to low levels by 15-20 years after planting. Multivariate analysis indicated that plantations occupied by nightjars are characterised by having greater areas of fine debris, moss, short grass, long grass, bracken and shrubs. Radio-tagged nightjars selected grass heathland and

young plantations, especially those 3-5 years old, during periods of activity. It should be noted that some habitats, such as deciduous woodland, which have been shown to be selected in other studies are scarce in this region. Likelihood of occupancy of plantations increased with proximity to 3-5 year plantations and decreased with proximity to 11-15 year old plantations. They concluded that the area of preferred foraging habitat close to a compartment (a permanent, geographically recognisable unit of forest) influences its chance of occupancy. Nightjars were also more abundant on plantations of acid soil type because acid soils inhibit vegetation growth leaving bare ground for nesting. Finally, there was circumstantial evidence that nightjar abundance increased with increased numbers of previous sprays of glyphosate on 6-10 year old plantations.

Work by Scott *et al.* (1998) on a nightjar population nesting on upland pine plantations showed that they preferred nest sites with more herbaceous cover associated with a more open aspect and occupied larger plantations.

More recent work on habitat utilisation by nightjars has been conducted both in the UK (Cross *et al.* 2005; Sharps 2013; Lowe *et al.* 2014) and in Europe (Sierro *et al.* 2001; Wichmann, 2004; Verstraeten, Baeten and Verheyen, 2011). A recent PhD study by Sharps (2013) is the most comprehensive study of habitat utilisation by nightjars in the UK. Her study focussed primarily on home range analysis and foraging behaviour in relation to nesting cycle and habitat quality as well as censusing and song territory analysis. Nightjar home ranges were an order of magnitude larger than the song territories of paired males, highlighting the importance of habitat outside the territory as a foraging resource (Sharp 2013). Some of the key findings of these studies will be discussed in more detail in the respective subsequent chapters. An upland population of nightjars in Wales preferred clearfells aged from 4-9 (9 out of 13 nests) but whether these had been replanted is unclear (Cross *et al.* 2005). Habitat utilisation has also been studied on the Continent. Three radio-tagged male nightjars in the Swiss Alps showed a preference for oak scrubland and avoided pine forest and steppe, but the researchers were unable to distinguish

between habit used for nesting and habitat used for foraging (Verstraeten *et al.* 2011). The point here is that findings in these studies are often very site specific or based upon very small samples and none of these studies have systematically measured the effects of disturbance or predation on habitat occupancy.

More recently the research focus has shifted towards the effects of disturbance at different spatial scales on habitat occupancy and nest success (e.g., Liley and Clarke 2003, Mallord *et al.* 2007, Lowe *et al.* 2014). Studies of nightjar breeding success (Murison 2002, Langston *et al.* 2005) have shown that nest success is lower on more urban heaths and that nests closer to footpaths are more likely to fail. Liley and Clarke (2003) found a negative correlation between site occupancy and the density of housing surrounding the site. A larger scale study by Liley *et al.* (2006) explored the relationships between housing levels, recreational access and nightjar abundance and distribution across approximately 18,000 ha of heathland and associated habitats in Southern England. They also found a negative correlation between nightjar numbers and housing density and this relationship was evident up to 5km away from the patch boundary. This was most marked on the Thames Basin Heaths, where for 19 of 20 patches, nightjars showed a preference for areas of relatively low visitor pressure, but these areas were also further away from the patch edge (than random points on the patch). Finally, at a single site Lowe *et al.* (2014) looked at the effects of recreational disturbance on habitat occupancy by nightjars in Sherwood, concluding that nightjars avoided 'disturbed' areas but this will be considered in more detail in Chapter 3.

1.1.3.iii. Breeding and Territoriality

The breeding season is usually from early May to the end of August but this may vary with geographical location, (latitude, longitude and altitude) lunar cycle (Perrins & Crick, 1996) and weather conditions (Berry 1979). They typically lay a clutch of two eggs and are single or double-brooded (Cramp 1985). Notable research on nightjar breeding behaviour was conducted by Heinroth (1909) and Lack (1929, 1930, 1932). The latter studies were based

on observations of only a few nesting pairs and the former was of a captive pair. Both found evidence that nightjars were double-brooded and males brooded the chicks from the first nest during the day allowing the female to incubate the eggs. Lack (1932) noted that second clutches were not near (>30m) the first nest and this may have implications for the size of song territories.

The nightjar defends an unusually large territory (range 1.5 to 31.9 ha) (Cleere and Christie 2016) if one considers that it is not typically the primary source of food (Brown 1964). However, territory size estimates might be unreliable because they might include foraging areas and represent home ranges rather than song territories. Relative to other types of avian territories this is rare and is shared by few other species, one of which is the reed warbler, (*Acrocephalus scirpaceus*) (Hinde 1956). Various functions for such a large non-feeding territory may include predation avoidance and reduced risk of extra-pair fertilisations. Maintaining territory boundaries an optimal distance from nest sites might reduce intrusions and extra pair copulations by neighbouring males. Nightjars actively defend their song territories by singing or displaying to and chasing other males. They also defend nests either by enhancing crypsis through incubation, distracting predators away from nests by feigning injury, or hissing and fly-hopping (short low level flapping flight interspersed with brief contact with the ground), or chasing predators/threats away (Cleere 1998).

In summary, the nightjar remains, of conservation concern and the factors that are responsible for its continued decline in some regions, or lack of range expansion in others, are still poorly understood. The ecological work in Chapters 3 and 4 aims to: understand how nightjars use commercial pine plantation, why they have become so important for breeding nightjars and to understand some of the ecological processes that lead to nest predation.

1.1.4. Molecular phylogenetics

Inclusion of molecular data, from single genes to entire genomes, in the studies of avian systematics has revolutionised our understanding of the relationships between all the major groups of birds. Two multi-order, genome wide studies were published in 2014: one produced a highly supported avian order phylogeny that resolves many debates on the timing and topology of their radiation (Zhang *et al.* 2014); the other, a comparative genomic analysis explored avian genome evolution and the genetic basis of complex traits (Jarvis *et al.* 2014). A third study by Prum *et al.* (2015) using an unprecedented 390,000 bases of genomic sequence data representing all major avian lineages provides a fully resolved phylogeny showing divergences that are congruent with the palaeontological record, supporting a major radiation of crown birds (a clade, consisting of a species and all its descendants) following the Cretaceous–Palaeogene mass extinction.

Until very recently, at lower taxonomic levels, the systematics of many groups remained poorly resolved. One such group is the Caprimulgiformes-Apodiformes complex. Analyses of these Orders suggested that they were not monophyletic (Ericson *et al.* 2006; Hackett *et al.* 2008; Braun & Huddleston 2009; Mayr, 2010; Jetz *et al.* 2012) and further work was required to resolve them. However, recent phylogenetic hypotheses for Neoaves firmly places the Caprimulgiformes and Apodiformes into the larger group Strisores, while resolving the paraphyly of the caprimulgiform families (Prum *et al.* 2015). At the level of family, much work is still required. Incomplete and in some cases poorly supported phylogenies exist for certain groups including the trochilids - hummingbirds (i.e. Bleiweiss *et al.* 1997; Gerwin & Zink, 1998; McGuire *et al.* 2007), apodids - swifts (Thomassen *et al.* 2005), aegothelids - owlet nightjars (Dumbacher *et al.* 2003), nyctibiids - potoos (Mariaux & Braun, 1996), and caprimulgids (Barrowclough *et al.* 2006; Larsen *et al.* 2007; Han *et al.* 2010). The focus has been on New World species, however, to understand the evolutionary and historical processes that have shaped the diversification of these groups in terms of their specific morphologies, ecologies and behaviour a study incorporating

more Old World taxa and more subspecies is overdue (Sigurðsson and Cracraft 2014). The aim of this chapter is to resolve the relationships between members of the *Caprimulgidae*.

The nightjars (*Caprimulgidae*) are the most speciose family within the Caprimulgiformes with 100 species in 17 genera and have a cosmopolitan distribution, with the Neotropics and tropical Africa particularly important areas of high diversity (Holyoak 2001, Dickinson *et al.* 2003). As with many other bird families, intraspecific diversity is high among caprimulgids, with multiple species further split into subspecies (Holyoak 2001, Dickinson *et al.* 2003, Cleere 2010). However, due to a highly conserved morphology, genetically divergent species have traditionally been lumped together, whereas phenotypically divergent but genetically similar species have not (Larsen *et al.* 2007).

1.1.4.i Phylogenetic Comparative Method

Many ecological, evolutionary and behavioural questions about form and function cannot be answered through experimentation alone due to the long-term macroevolutionary processes involved (Freckleton 2009). To attempt to answer them one needs a phylogenetically controlled approach which uses information on the evolutionary relationships of the organisms i.e. phylogenetic trees, to compare species (Felstenstein 1985; Harvey and Pagel 1991; Garland, Harvey and Ives 1992). The most common applications of phylogenetic comparative methods (PCMs) is to test for correlated evolutionary changes in two or more traits, or to determine whether a trait contains a phylogenetic signal, namely, the tendency for genetically related species to resemble each other (Blomberg *et al.* 2003). The most commonly used comparative tests to control for phylogenetic nonindependence are independent contrasts (Felstenstein, 1985) and generalised least squares (e.g., Pagel 1997, Garland *et al.* 1999; see Garland and Ives 2000 for comparison). For example, Gartner *et al.* (2010) used phylogenetically independent contrasts (PICs) to examine the position of the heart in terrestrial and arboreal snakes. However, there are several applications of PCMs to particular questions about long-term processes including the assessment of phenotypic trait variation in relation to rates of

speciation (Harvey and Rambaut 2000) and/or extinction events (Harvey and Rambaut 1998). Although most studies that employ PCMs focus on extant organisms, the methods can also be applied to extinct taxa and can incorporate information from the fossil record. This gives them considerable power because they can map ancestral state reconstruction and identify causes of loss and/or gain of traits and occurrence of key evolutionary innovations.

1.2 THESIS OUTLINE

My research comprises two main areas of investigation. The first is a species specific study of the nightjar, with reference to habitat selection for nesting, and factors affecting predation including researcher activity. The second is a genetic analysis of species taxonomy of the nightjars, Order Caprimulgiformes, Family *Caprimulgidae*, using mitochondrial DNA, and the analysis of facial bristles using a phylogenetically controlled comparative method.

1.2.1. Ecological work

The nesting and foraging ecology of the nightjar nesting in the UK (and increasingly Europe) is reasonably well-studied (Lack, 1931; Ravenscroft, 1989; Burgess *et al.* 1990; Alexander and Cresswell 1990; Bowden and Green 1991; Kenyon, 1998; Sierro *et al.* 2001; Wichmann, 2004; Cross *et al.* 2005; Verstraeten, Baeten and Verheyen, 2011; Sharps, 2013). However, these studies have shown that populations breeding in different habitats have quite varied ecologies in terms of their nesting and foraging habitats and behaviours and all of the studies have relied on close-contact with the study organism. A more complete knowledge of the role of habitat selection and the effects of researcher methods on predation is required to provide an evidence base to guide subsequent studies and to inform conservation initiatives.

Study sites

The studies took place between mid-April and late August of 1994 in the 1,380 hectare coniferous plantation known as Sherwood Pines Forest Park located on the Bunter Sandstone series between Worksop and Hucknall, in Nottinghamshire, the UK and between mid-April and late August of 1998 in the 1,540 hectare coniferous plantation known as Wareham Forest (and surrounds Gore Heath and Morden Bog Nature Reserve - 1,808 ha) located on tertiary deposits in the Poole basin, Dorset, the UK. Although leased and managed by the Forestry Commission for commercial timber production, both sites are major heathland, and associated wildlife initiatives, whereby felling is designed to accommodate and enhance wildlife interests through the FCs 'Open Forest Policy'. Sherwood Pines Forest Park is a designated 'Site of Importance for Nature Conservation', a local nature conservation designation. Wareham Forest has conservation status under SPA, SSSI, RAMSAR and SAC status. It encompasses Morden bog, which is a designated 'biogenetic reserve' and NNR. The sites support just under 1.7% and 6.3% of the UK nightjar population estimate of 4,131 birds in 2004 (Conway *et al.* 2007) respectively and their populations have remained largely stable although the Sherwood population had incurred a 10% drop since 2001 (Lowe *et al.* 2014).

Both are heterogeneous landscapes, containing a mosaic of semi-natural and managed habitats. The managed habitats include the conifer plantations which are characterised by different commercial species in different growth stages with varying canopy cover, ranging from fully mature pines to unplanted clearfell. Semi-natural habitats include bog, grassland, lowland heath, deciduous firebreaks and arable land. The wide variety of habitats in the study sites therefore provides an ideal location in which to conduct investigations into nightjar nesting habitat preference. There is also the opportunity to examine how nesting habitat affects reproductive success. Finally, in light of the conservation status of the nightjar and its apparent 'popularity' as an organism to study, such close and detailed examination of its ecology and behaviour will allow us to assess whether our research is impacting upon the species.

1.2.1.i. Aims

In these studies the aims were to measure the:

- effects of capture techniques on the breeding behaviour of instrumented birds
- effects of backpack mounted radio transmitters on breeding behaviour
- effects of blood sampling on breeding behaviour and chick growth
- song territory characteristics of nesting nightjars
- effects of habitat selection and degree of visitation on predation of real and artificial nightjar nests

To acquire data on song territory characteristics I conducted fieldwork using tail-mounted and back-pack harness radio transmitter. Although the backpacks have been used on other avian species this was the first time they had been deployed on nightjars so I had to monitor their effects on the instrumented birds. In order to catch the nightjars for instrumentation mist nests were used. This is the traditional method for trapping nightjars but again no research has been carried out to determine the potential effects of this practice. Finally, blood samples were taken from focal birds for a mating system and population study (not included in this thesis) so the effects of this were also measured.

The final aim is to provide species specific guidance for researchers to minimise the effects of fieldwork activity on nightjars and advice for habitat managers who have responsibility for sites with breeding nightjars.

1.2.2. Phylogenetic and comparative method work

I highlighted above that the systematics of the nightjars is not fully resolved and at the time of writing, no family level phylogeny for the *Caprimulgidae* existed. This study uses the mitochondrial gene, cytochrome *b*, (*cyt b*), to test the relationship between members of the family *Caprimulgidae*. The lack of family level molecular phylogeny was the impetus for this particular study and this (in part) provided the opportunity to map morphological

and behavioural characters onto the tree in order to understand their distribution, evolution and potential for speciation in the group. One character was selected, head bristles, which occur in all five families in the traditional classification of this Order with the focus of the analysis on the *Caprimulgidae*. In a review of head bristles in birds Larsen (in litt) found that bristles occurred in over 65 families, but the function and taxonomic distribution of bristles has not been studied systematically.

1.2.2.i. Aims

The relationships amongst members of the Caprimulgiformes and in particular the family *Caprimulgidae*, remains ambiguous with limited consensus about the basal positioning of *Lyncornis* and *Eurostopodus* (e.g., White *et al.* 2006). This is also true for the lower level taxonomic relationships. I aim to:

- test whether the genus *Caprimulgus* is monophyletic.
- explore the relationships between other genera.
- use a composite phylogeny to map the distribution of facial bristles in the Caprimulgiformes.
- propose theories for the function and evolution of facial bristles in the Caprimulgiformes.

1.2.3. Chapter Outline

Chapter Two's focus is the welfare of the study organism and represents a systematic attempt to gauge the impact of the research methodology on nightjar ecology and behaviour. Chapter Three, is principally ecological and behavioural and aims to determine the nesting requirements of plantation nesting nightjars and Chapter Four assesses whether habitat choice and disturbance play a measurable role in nest predation rate and nest survival. Chapter Five represents the first major molecular phylogeny of the Caprimulgidae and Chapter Six employs the comparative method to examine a morphological trait within the group, facial bristles.

The first chapter after the introduction is the initial data chapter (Chapter Two). It explores the effects of the research methodology on various aspects of nightjar ecology and behaviour including breeding success, predation, chick growth and philopatry. In order to undertake the applied ecology element of this thesis the author used mist nets and tape lures, attached tail mounted and backpack radio transmitters, located nests and took blood samples via brachial or jugular venepuncture. Bleeding was undertaken under a Home Office licence. Due to the potentially high level of interference with the focal animal coupled with its conservation status, the author was required by the British Trust for Ornithology (BTO) and English Nature to monitor the effects of blood sampling and backpack harness radio transmitters on nightjars during the first fieldwork season. After completing the preliminary monitoring and reporting findings to the BTO we proposed protocols for working ethically with nightjars.

The habitat selection study, Chapter Three, also involved the attachment of radio transmitters to adult nightjars during the two breeding seasons to determine their nest site and territory characteristic. Censusing nightjars has traditionally been done using either territory mapping to count singing males, radio tracking and more recently using capture-recapture models (Jiguet and Williamson 2010). Although radio tracking has been used to study nightjars before, this is the first time that accurate measurements of territory have been related to reproductive success in relation to nest predation. Chapter Four explores the relationship between habitat selection and predation rate using artificial nests. Nest site choice and characteristics were based on the findings from natural nests (Chapter Three). Predation rates were compared by habitat type (age class of plantation, or vegetation type, i.e. grass, bracken, heath), egg type (nightjar, quail and plasticine), land geometry (i.e. area of nesting habitat, compactness ratio, proximity of nest to habitat edge) and whether the nest had been visited by the researcher.

The species-level analysis (Chapter Five) involved the sequencing of the mitochondrial cytochrome *b* gene. The aim of the study was to include taxa from as many different

caprimulgi genera as possible, and to use the partial sequence of cyt *b* as a probe of *Caprimulgidae* phylogeny. This study included twenty-one nightjar species, from ten genera, but with most species belonging to the family *Caprimulgidae* and represents the first major molecular phylogeny of the nightjars.

Chapter Six used the molecular phylogeny above, combined with more contemporary phylogenetic hypotheses for this group, to map the distribution of facial bristles across the Caprimulgiformes, and with specific emphasis on the *Caprimulgidae*. Morphometric data were collected from bird skins collections (and to a much lesser extent, photographs) at Natural History Museum Tring (NHM Tring), World Museum Liverpool (WM Liverpool) and Natural History Museum (NHM Manchester). This study used the comparative method controlling for phylogeny and proposes functions for these characters

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CHAPTER TWO

GENERAL SAMPLING METHODOLOGY AND ITS EFFECTS ON NIGHTJAR WELFARE

Abstract

Procedures that affect the welfare of animals raise ethical considerations and can compromise research objectives by introducing bias into data collection but many studies assume that the study organism is behaving naturally. Knowledge that one's research is affecting the behaviour of the study organism is even more important when it is of conservation concern. Furthermore, it is not possible to determine acceptable levels of risk for a research method until a proper evaluation of research-related injuries and mortalities has been conducted. This study assessed the impacts of the research methods of mist netting, radio tagging and blood sampling on two populations of nightjars. Vertical mist netting and drop-netting resulted in 0.75% mortality but had no measurable effects on adult nightjars including no signs of capture myopathy or abandonment of their nests or territories after capture. Radio tagging and telemetry had no measurable long-term effects on breeding success, philopatry or survivorship of nightjars. The mean fledglings per breeding attempt (FPBA) over six breeding seasons for non-instrumented birds in both forests was 1.21 chicks per breeding attempt based on 103 nests, compared to 1.29 over two breeding seasons for all instrumented birds based on 21 nests (tail mounted tags 1.28 FPBA and backpack mounted tags 1.33 FPBA). Return rates were similar for instrumented and noninstrumented birds. Short-term effects included premature moult of the central rectrice and small amounts of feather wear beneath the backpack transmitter of instrumented birds. With regard to blood sample collection, only short-term effects such as bruising and lethargy were recorded. Bled chicks experienced a reduction in weight, and slower weight gain than non-bled siblings. Bleeding also reduced wing growth rates. Adult nightjars experienced no measurable long-term effects as a result of bleeding, with a comparable breeding success to non-bled birds and comparable return rates in subsequent breeding seasons. The conclusion is that controlled mist-netting, radio tagging and small volume and infrequent blood sampling do not adversely affect breeding nightjars.

2.1. INTRODUCTION

Experimental procedures that potentially affect animal welfare raise ethical considerations. They may also undermine research objectives by introducing bias into data collection and should therefore be considered when interpreting results. Furthermore, one cannot establish satisfactory levels of risk for a sampling method until a proper evaluation of research-related injuries and mortalities has been conducted (Wilson and McMahon, 2006). In this Chapter the potential effects of the research methods involved on the welfare of nightjars are considered. The three main areas of investigation are the effects of:

1. capture technique on adult and juvenile nightjars.
2. radio-tagging on adult nightjars
3. blood sample collection on adult and juvenile nightjars

The first section describes the most effective capture techniques for specific birds, e.g., territorial males, brooding females and outlines a best practice guide to minimise disturbance. The potential harm caused by the different capture techniques, mist-netting, flushing into static net, and drop-netting is also considered. Surprisingly few studies have considered the effects of capture using mist nets (Spotswood *et al.* 2011, Kania 1996) so the section begins with a review.

The radio tracking experiments were primarily designed to provide ecological data on habitat use of plantation nesting nightjars and to provide an evidence base for 'The Forestry Commission' habitat management strategy for the nightjars in Sherwood forest. Although data on home range and habitat use were collected the results are not presented in this thesis. Only data pertaining to song territory (including nest sites) is included and used in subsequent chapters. There has been a significant amount of interest in the effects of tagging on instrumented animals (Barron, Brawn and Weatherhead 2010) and salient studies are reviewed.

Finally, because blood samples were collected in order to determine the population structure and mating system of the nightjar (not included in this thesis), the effects of bleeding on the behaviour of adults and the growth rates of chicks were assessed. Few studies have attempted to quantify this (Voss, Shutler and Werner, 2010) and these are reviewed in an introduction to the section.

2.2 GENERAL METHOD

These studies

Between 1994 and 1998, 156 birds were caught using either vertical mist netting (n=138), flush into static net (n=13) or drop-netting (n=5) techniques. Two different types of radio transmitter were fitted to 30 adult nightjars during the breeding season in 1994 and 1998. The 1994 fieldwork took place in a commercial pine plantation in Nottinghamshire and used conventional tail-mounted radio transmitters, whereas the 1998 fieldwork, also in a pine plantation, took place in Dorset and used both tail-mounted and back-mounted harness radio transmitters. Blood samples were collected from 49 adult nightjars and 61 chicks during 1994, 1995 and 1998. Sample sizes for sexes and age classes are detailed in section (2.2.3.i). Fieldworkers involved in nightjar capture and tagging possessed endorsements on their standard ringing license, which included “authorisation to use tape lures in the breeding season for nightjar” and “authorisation to use traps, decoys and radio transmitters (tail and backpack) on adult nightjars.” Brian Cresswell (permit number FC4028) C. Larsen was supervised to take blood samples by Professor David Parkin (University of Nottingham) under a Home Office license (awaiting reply).

2.2.1. Capturing nightjars

This section describes the methods for trapping and tagging individuals. Male nightjars were targeted for capture but selected females were also targeted where the nest location was unknown. Male nightjars are territorial and usually respond to perceived threats such as other singing males with singing, wing clapping and ruddering (flying with tail fanned at 90 degrees to body) and aerial pursuit (Cleere 1998). Certain birds are so

territorial that they will even respond to human hand-claps, performed to mimic their wing-clapping display. Even the waving of a white handkerchief may elicit a territorial response. By using a tape recording of a churring (singing) male one can exploit this and elicit territorial behaviour. The timing of mist netting is critical because the more territorial a bird's behaviour, the more likely a successful capture. Therefore, the optimal period for catching is the beginning of the breeding season, normally early May, when males are arriving on the breeding grounds and establishing territories and when males are brooding first broods. To the authors knowledge there is no published evidence that unpaired males are more or less responsive to tape lures but this may have affected randomness of sample (reference).

Working closely with nightjars allows researchers to determine, anecdotally, whether or not a male has a mate, and to a degree, his stage in the nesting cycle. Such knowledge is useful when conducting research using mist netting. Newly arrived males have a characteristically weak and disjointed churring song and are less responsive to the tape lure (juveniles males - hatched that year - also have similar songs but won't be heard until late in the breeding season). Mated males would be seen flying with a female within their breeding territory and are strongly territorial, and respond 'instantly' to the tape recording if female is not incubating. Unmated males were rarely seen with a female in their song territory although mated females did occasionally visit unmated males. Once the female is incubating, males spend more time foraging and have regular long feeding bouts after dusk and before dawn. In contrast, unmated males did not appear to have a consistent feeding period. Mated males chur at dusk, into the early part of the night and again at dawn, or in response to rival males in the territory. In contrast unmated males sing early in the evening and throughout the night and are responsive to the tape recording consistently throughout the breeding season. Mated males also typically display before nest change-over including wing-clapping display, butterfly flight and bubbling call after churring. Incubating females often replied with a 'croak' to acknowledge the male and would sometime leave the nest before he landed nearby. This was the most effective

way of locating nest sites. Mated males typically roost within 8 meters of the females but once flushed, or when the female has very young chicks, they are more likely to roost up trees c 15 meters above the ground. Finally, seasonal peaks in territoriality also occur when males establish a second brood and after the first brood fledges.

2.2.1.i Mist-netting

The use of mist-netting to capture wild birds is a commonly used technique with over 1.2 million birds banded annually in the US (Bird Banding Laboratory, 2014) and nearly 4 million across Europe (EURING, 2007). Despite the number of birds that are captured in this way the number of studies that have tested the assumption that birds are unharmed is not commensurate. A study by Jennings *et al.* (2008) found that wrenit (*Chamaea fasciata*) nestlings from nests near to less frequently used nets were in poorer condition than those from nests close to frequently operated nets and also than chicks from nests far away from any nets. They also found that song sparrow (*Melospiza melodia*) daily survival was higher where at least one parent was captured while the nest was active. For all other comparisons including duration of handling time and breeding condition (i.e. size of brood patch) there was no evidence that mist netting had an adverse effect on reproductive performance. However, a review by Spotswood *et al.* (2011) found evidence that bird species varied in their susceptibility to injury and mortality with large species more at risk of injury and predation and smaller species more prone to stress and tangling-related injury. Average rates of injury were 0.59% and of the 36 most commonly captured species, four species had high rates of injury and predation relative to the mean. For example, spotted towhees (*Pipilo maculatus*) and Allen's hummingbirds (*Selasphorus sasin*) were more prone to stress, whereas Western tanagers (*Piranga ludoviciana*) and American robins (*Turdus migratorius*) were more prone to wing strain. Average mortality was 0.23%, and therefore lower than the 1% target rate specified in Ralph *et al.* (1993), and survival of injured birds was comparable to non-injured birds.

One of the main side-effects of capture using mist nets is self-injury and capture myopathy (Cox and Alton, 1998; Hofle *et al.* 2004; Marco *et al.* 2006, Mulcahy *et al.* 2011), which is characterised by damage to muscle tissues caused by strenuous use of the large appendicular muscles during capture (Williams & Thorne 1996). The effects of this can be long lasting if handling and restraint times are not kept to a minimum (Nicholson *et al.* 2000; Ponjoan *et al.* 2008, Ruder *et al.* 2012). Some bird species, such as divers, Yellow-billed Loons (*Gavia adamsii*) and Pacific Loons (*Gavia pacifica*), are particularly susceptible to increased fitness costs incurred by capture and even attempts to reduce such costs through modified capture techniques results in high nest failures (Uher-Koch, Schmutz and Wright, 2015).

Finally, in a review of the effects of mist-netting by Spotswood *et al.* (2001) found that different ringing groups had separate conventions for reporting incidents, and within-group reporting was not always consistent implying that not all incidents of injury or death were reported consistently.

Mist-netting is the most effective and least obtrusive way of catching both adult male and female nightjars (Squire & Alexander 1981). In simple terms, mist-netting involves luring the focal bird into a vertically erected fine mesh net by playing a recording of another bird singing. Territory holding nightjars perform a series of low gliding flights over the tape recorder, sometimes even landing on it. The tape recorder was placed beneath a 10 meter mist net erected between two poles. The net specifications were; The most effective placement of mist nets was at a right angle to vegetation edges, provided the vegetation was equal to or higher than the mist net. Even at typically low light levels, nightjars are still able to see the fine mesh of the net. Birds would often fly toward the tape at considerable speed and on detection of the net were able to either flip over the top or stop dead in front of it and hover. Unless the nightjar was responding aggressively to the tape, more often than not it was able to avoid entrapment. This problem is exacerbated if the backdrop to the net is paler than the mesh, and nets set against the evening sky were

rarely successful. Therefore where possible, nets were erected in front of dark backdrops such as bracken, heather or conifers.

Tension was judged carefully since with low tensions the mesh gathered into dark, visible streaks and with high tensions, birds hitting them at speed would tend to bounce off and not fall into the pockets. Getting the tension 'wrong' would require further catching attempts and therefore further disturbance. Similarly, an optimal net height was determined to prevent target birds overshooting. Using nets with 4 pockets allow nets to be set at the maximum optimal height while still allowing pockets to form.

However, concerns over the effects of prolonged tape-luring on territory establishment meant that we limited the length of the tape-playing to half an hour per catching attempt. If after that time we had not caught the bird we attempted to catch elsewhere. Subsequent catching efforts for focal birds did not take place for a minimum of five nights to allow the bird to establish its territory.

2.2.1.ii Flush into static net

Nests that were located in tall vegetation could not be drop-netted (see 2.2.1.iii.). An alternative way to catch the adult was to erect the net vertically (as above) close to the nest. To increase catching efficiency, two ten-meter nets were erected in a chevron formation. The aim was for a group of fieldworkers to form a semicircle and walk towards the nest slowly in the hope of flushing the adult into the net. When a brooding bird is disturbed from its young it will usually perform a distraction display (spread wings and tail, short hopping flights colliding deliberately with the vegetation), in which it feigns injury. The birds seem to be distracted by the intruders to the extent that they don't see the net. This capture technique reduced the risk of standing on fleeing chicks and moved the capture process away from the nest.

2.2.1.iii Drop-netting

The procedure is more difficult to perform than the passive 'sit and hope' or 'flush into static net' technique of vertical mist-netting, and relies on actively taking the net to the bird. It usually involves at least three fieldworkers; two carrying the net and a third (who has the major role in catching the bird) guiding them towards the nest.

The mist-net is suspended between two poles that are held overhead in a horizontal position. The net should be erected some distance from the nest patch to avoid alerting the brooding adult. The net can be transported towards the nest vertically (this reduces the risk of it snagging on vegetation or brash), but this relies on keeping it taut. As the nest is approached the 'guide' gestures to the net carriers to position themselves to achieve maximum coverage of the nest patch and the net is flipped horizontally. Occasionally the incubating bird will fly off before the net is lowered onto the nest patch. If the vegetation is too high around the nest birds also avoid capture by flying underneath the net and away through gaps in the vegetation.

We drafted a code of conduct for performing this activity, including:

- Accurate knowledge of the status of the nest. Personal communication with other fieldworkers (Cresswell pers.comm.) has shown that females may abandon their eggs if they are drop-netted too early in the breeding cycle. The ideal age of the chicks should be around nine days old. At this age the chicks will be breaking-pin, i.e. their primary flight feathers will be emerging from the protective sheath, and are thus suitable for ringing. Most importantly, desertion by the female does not occur.
- Weather conditions should be suitable. Precipitation must be avoided as should conditions of high solar radiation. The adult may not return to the chicks until dusk and hypothermia or desiccation may result in death of the eggs/chicks.
- Attempting to catch in windy conditions will probably result in failure as the sitting adult may see the net moving and escape. This would result in a subsequent catching attempt and therefore further disturbance and stress.

- In all cases, minimise the time the adult will be away from the chicks. This can be achieved by drop-netting in the early evening. However, the adult will become more alert as light levels drop so they will be more difficult to catch.
- Prior to placing the net over the occupied nest, it is important to establish where the chicks are sitting and which way they are facing. It should be the role of at least one person to observe the movements of the chicks after the net has been lowered into place as the chicks can run or fly-hop some meters.
- Once the net is in place do not rush in to grab the adult as this might damage the nest area or one might stand on a fleeing or unseen chick. Allow the female to become entangled in the mist net.
- No predators in the vicinity. Drop netting should be avoided if there are visual predators in the area. Evidence suggests that corvids associate human presence with food and forage where they have observed human activity (Marzluff and Neatherlin 2006).

2.2.2 Territory mapping and Radio-tracking

Two commonly used methods for determining habitat use in wild animals are radio-tracking (White and Garrott, 1990) and territory mapping (particularly birds) (Bibby 2000). The latter relies on recording the locations of singing males on a map to delineate song territory (Bibby 2000), whereas radio tracking allows an instrumented animal to be tracked continuously or in sampling bursts (White and Garrott, 1990; Kenward, 2000). Each method has advantages and limitations. For example, territory mapping is time consuming and the mapped territory is biased towards song posts. This is problematic because song output varies during the breeding season leading to differential detection of birds and in particular paired and unpaired males. Tracking requires the capture and instrumentation of the focal animal which one then has to follow, which is both time consuming and limits the number of individuals that can be tracked.

The utility of 'tracking' for studying the movements of wild organisms is well-established (White & Garrott, 1990) and a diverse range of species from whales (Mate *et al.* 1999), to wolves (Berger *et al.* 2008) have been tracked. Modes of tracking are equally diverse, and include traditional VHF radio tracking, satellite tracking and global positioning system tracking. Satellites have been used to track the migratory pathways of loggerhead turtles (*Caretta caretta*) (Timko and Kolz 1982), and GPS tracking has mapped the migration routes of some remarkable long-distance migratory birds, e.g., bar-tailed godwit (*Limosa lapponica*) (Gill *et al.* 2009).

One of the major problems with studies of habitat utilisation is the unavoidable bias introduced by the researcher when attempting to find roosting or nesting birds. Without tracking equipment, the best that can be managed in the field is a systematic search of potential habitats, followed by attempts to flush out individual birds. Invariably, this technique will underestimate the population and miss birds that are roosting up trees, or sitting in impenetrable vegetation or habitat deemed unsuitable by the researcher. To remove the bias introduced by the likelihood of a bird being located by chance, one has to be able to detect the bird at will. This can be achieved by fitting a small radio transmitter to the organism and tracking it from a remote position with a receiver.

Monitoring the bird's activity from a remote position with a receiver, or with a data-logger, may reduce the chances of the investigator affecting the normal behaviour of the individual under study. Furthermore, even with night-vision equipment, nocturnal animals such as nightjars are difficult to follow (SRG 1988). However, once familiar with the organism under study, tracking can be used to determine where the instrumented animal is, and even what it is doing.

In summary, the results of territory mapping and radio tracking are likely to provide different estimates of habitat use, with territory mapping identifying the habitats within the song territory and tracking providing all habitats that the animal visits, including those

outside the breeding territory (Anich *et al.* 2009). Territory mapping might overestimate singing males if a species is particularly mobile (Thompson 2002, Gregory, Gibbons and Donald 2004), and underestimate them if they are skulking (Bibby 2000, Remsen 1994) or difficult to observe (Health *et al.* 2008) or if their territories overlap (Bibby 2000) and they share song posts. On the other hand, radio tracking can identify individuals and distinguish between tagged, and untagged birds, as well as unmated males (Amrhein, Kunc and Naguib 2004). Telemetry allows fieldworkers to study both instrumented and noninstrumented birds as part of the same study because it allows researchers to distinguish between them. Hence in this study, we employ a combination of territory mapping and radio telemetry to study the song territory of the nightjar.

2.2.2.i Telemetry and birds

Instrumentation of wild birds might lead to associated fitness costs resulting in higher mortality, nest abandonment, behavioural modifications or loss of physical condition (Kenward 2000, Barron *et al.* 2010). However, the majority of tracking studies appear to adopt the assumption that tagging does not affect an animal's behaviour and therefore that the tagged organisms are representative of the population under study. This assumption may be necessary in cases where an animal cannot be detected by any other means than tagging, or that the associated risks are compensated for by the benefits derived from the application of the research results to the conservation of the studied species (Wilson and McMahon 2006). However, in some cases measurable effects are detectable and should be assessed (Cox & Afton 1998, Ponjoan *et al.* 2008), so that risks can be evaluated and reduced (Wilson & McMahon 2006, Spotswood *et al.* 2012), particularly in species of conservation concern (Casas *et al.* 2015). In a review of 84 studies that had attached transmitters to birds, Barron, *et al.* (2010) found that instrumented birds had markedly higher energy expenditure and were much less likely to breed. For example, the duration of foraging trips increased in instrumented Humboldt penguins (*Spheniscus humboldti*) (Taylor, Leonard and Boness 2001) and Orbrecht, Pennycuick and Fuller (1988) found that back-mounted radio-transmitters increased drag in wind tunnel

experiments on waterfowl and raptors. Robert, Trolet and Savard (2006) found that female Barrow's goldeneye (*Bucephala islandica*) spent more time preening and less time provisioning young when fitted with a backpack harness.

Capture myopathy is the most common side-effect of tagging but this has been detailed above. The potential trauma (e.g., shock moult in birds) caused during capture, or the process of attachment, may cause reduced nest attendance (e.g., sooty shearwaters (*Puffinus griseus*), Söhle, *et al.* 2000) or an incubating female to abandon her eggs or desert chicks (Klomp and Schultz 2000, Hedd *et al.* 2001), and thus have a significant reproductive impact (Philips, Xavier and Croxall, 2003). Territory holding ability of tagged males may be compromised by a male's preoccupation with the tag and instrumented birds might even abandon their territory as was found in golden eagles (*Aquila chrysaetos*) (Lockart & Kodiart 1979). Another frequently reported cost to fitness is an increase in comfort movements, e.g., preening and shaking (Greenwood and Sargeant 1973). Disproportionate amounts of time spent preening, etc. may reduce the effort dedicated to foraging or breeding behaviour (Hirons and Owen 1982) resulting in weight loss (Perry 1981) or nest failure (Amlaner *et al.* 1979). Devices may indirectly reduce the fitness of non-instrumented mates if they compensate for decreased parental investment by the instrumented bird (Paredes, Jones and Boness, 2005).

Devices have also been shown to cause feather loss and skin damage, which might compromise insulation (Hines and Zwickle 1985). Other effects on instrumented individuals include entanglement caused by loosely fitted harnesses (Hirons and Owen 1982) and whip antennas becoming entangled in vegetation or causing electrocution of birds that use power lines (Dunstan 1977). Finally, reduced survivorship of instrumented birds or their offspring was demonstrated for the pheasant (*Phasianus colchicus*) (Warner and Etter 1983) and for willow ptarmigan (*Lagopus lagopus*) (Erikstad 1979), and chicks of instrumented tufted puffins (*Fratercula cirrhata*) gained less weight than those of non-instrumented adults (Whidden *et al.* 2007).

Both device design and experimental goals have been shown to cause variation in the effects on instrumented birds. White *et al.* (2014) reviewed studies on transmitter location in order to compare the effects of external transmitters to implanted ones, concluding that implants had fewer effects on behaviour compared to externally attached devices but see Hooijmeijer *et al.* (2014). Both design of the transmitter and the period of attachment may have markedly different effects on the instrumented bird. For example, small geolocators used for long term data collection have been shown to increase corticosterone and reduce body mass in common (*Uria aalge*) and thick-billed murres (*Uria lomviamurres*). However, survival rates in equipped birds was no different than in control birds and chick feeding rates were also similar between equipped and unequipped birds (Elliot *et al.* 2012). A study of the burrow nesting crab plover, (*Dromas ardeola*) during a three week incubation period fitted with GPS data-loggers showed no ill effects including normal activity, weight gain and reproductive success (DeMarchi *et al.* 2012).

If, in terms of fecundity, there are no observable effects of tagging on individuals, it would be erroneous to assume that the bird had not been affected in some way. A more sensitive measure might be the return rate in subsequent breeding seasons of tagged individuals compared to non-tagged individuals. Since successful nests are more likely to be reused in subsequent seasons (Cavitt *et al.* 1999), an additional measure of interest may be/is the level of re-occupancy of nests/territories of tagged individuals in relation to the degree of philopatry displayed by the population as a whole but there seem to be few studies on this subject.

The technique of tracking may also protract the period of disturbance. Remote monitoring using data loggers or satellites should lead to no post-instrumentation interference. However, radio tracking is often employed to measure the behaviour of reclusive species that avoid humans. Thus radio tracking will undoubtedly cause disturbance to the instrumented animal, especially if the experiment relies on the observer gaining visual

contact. Inexperienced trackers may encroach too close allowing the instrumented animal to detect them and consequently affect its behaviour. At the least, the observer may collect spurious data that is biased by his presence. However if such disturbances coincide with critical periods in the instrumented organism's life, (e.g., establishing a territory or feeding young) it may affect its natural behaviour so drastically as to reduce its fecundity.

2.2.2.ii Telemetry and nightjars

A number of studies using different transmitters and devices have now been conducted on nightjars (e.g., tail-mounted radio transmitters, Alexander and Cresswell, 1990; Sharps *et al.* 2015, and geolocators, Cresswell and Edwards, 2012). Such studies have provided important information on foraging habits and migratory behaviour, but to the author's knowledge, none has systematically measured the effects of instrumentation on the study organism.

Despite the findings from the previous studies on other bird species that radio-tagging causes changes in behaviour, physical harm and reduces fecundity, research involving the use of radio transmitters on nightjars has not demonstrated similar effects (e.g., Alexander and Cresswell 1990). Furthermore, the difficulty of studying a nocturnal and cryptic species such as the nightjar prohibits the use of techniques that rely on visual contact. However, conventional tail-mounted transmitters only locate the position of the instrumented animal, and provide limited information about the organism's behaviour so we also used backpack transmitters with underwing thermistors (Figure 2.1) (for measuring air temperature). The use of the backpack transmitters was undertaken for the first time and therefore required an experiment on a small sample of birds (for consideration by BTO unconventional marks committee) to assess its effects on the instrumented bird, before it could be used to monitor behaviour in the wider population.

2.2.2.iii Randomness of sample

A common method for achieving a random sample of a population for purposes of radio-tracking, involves instrumenting 'what is caught in the trap' (White and Garrott 2000, Kenward 2000) and this is the approach adopted in this study but many authors have shown age and sex bias likelihood of capture in other species (Brown and Brown 2009). Both this, and the fact that certain birds were targeted, particularly females when we were having difficulty locating the nest, may have biased the sample towards easy to catch males and females nesting in dense vegetation.

2.2.2.iv Tracking equipment

30 radio-tagged birds (Nottingham, n=15, Dorset, n=15) were tracked using a hand held Marinar 57 receiver and a three-way Yagi antenna, in order to determine their nest site locations, and song territory. A data logger and four Yagi antennas erected at right angles to one another, at a height of 20 m in a tree, was also used to monitor the behaviour of the Dorset birds, but with varied success. Therefore, only data from the mobile tracking method was used for analysis.

2.2.2.iv(a) Tail-mounted radio-tags

The tags employed in this study were modified versions of tags specifically designed for use on nightjars in a previous study by Alexander and Cresswell (1990). The tag weighed 1.2g and was well below the critical transmitter weight: body weight ratio (of <3% of body weight) determined by studies on other birds such as ducks (*Anas* species) (Greenwood and Sargeant, 1973) and pheasant (*Phasianus colchicus*), (Warner and Etter 1983). Male nightjars weigh between 51–101 g and females weigh between 67–95 g (Holyoak 2001) so tags weigh between 2.35% and 1.18% of male body weight and 1.8% and 1.26% of female body weight.

Prior to undertaking the fieldwork, C. Larsen was trained to fit the tail-mounted tags at Biotrack Ltd. Dorset. The technique involves two fieldworkers. The bird is held with wings

closed and the upper part of its body is contained in a ringers' bag to calm it down. Only its rump and tail are exposed. The shaft of one of the central retrices is cleaned at the base with absolute ethanol prior to attaching the tag. The tag has already been checked to determine its working condition and frequency. A small amount of superglue is deposited on the custom built groove in the epoxy resin on the underside of the tag, and the tag is placed onto the dorsal surface of the rachis, ~5 mm from the base of the retrace. It is held until the glue has dried sufficiently to keep it in place. A short length of dental floss is tied around the tag and the rachis of the retrace and knotted on the ventral surface. Finally, a small drop of super glue is deposited on the knot to ensure that the tag is held in place. The thin wire antenna is attached with dental floss to the end of the feather. The bird is inspected for damage and the tag re-tested before it is released. This procedure took no more than twenty minutes.

2.2.2.iv (b) Harness backpack with underwing thermistor

The study carried out in Dorset is the first to fit harness-mounted backpack radio transmitters to nightjars. The design and model 2.0g Biotrack TW-4/Ag393 backpack with underwing thermistor (Figure 2.1) was modified from harnesses originally developed for thrushes (Hill *et al.* 1999). The body weight of captured birds was weighed to determine if the tag exceeded the 3% rule (see above). If the bird was lighter than 65g the harness was not fitted. It involved two elastic wing loops that were fixed by a cotton thread 'weak link' such that both loops would open when the thread broke. The wing loops were made from 3 mm wide soft ribbon elastic, and each loop was fixed permanently to the tag at one end. At the other end of each loop, the elastic was tied to cotton sewing thread, which in turn was threaded into a tube built into the tag. The cotton threads from each loop entered the tube at opposite ends and both threads emerged from a hole in the side of the tube, where they were tied together when the tag was fitted to the bird.

The tags were equipped with temperature-sensing thermistors on short flexible plastic coated wire leads. The thermistors were sited in the axilla, and kept in place by being

bound to a wing loop. They were warmed under a closed wing, and rapidly cooled by the under-wing airflow when the bird flew. The effects of cooling and warming allow one to distinguish between a stationary bird with wings closed – constant slow pulse signal, and a bird in continuous flight – a fairly constant but more rapidly pulsing signal. Finally, periods of inactivity interrupted by bouts of flycatching were characterised by - slow and constant pulse, interspersed with abrupt and rapid fluctuations in pulse strength.

Although the size of the wing-loops could be increased by stretching the elastic, it was impractical to fix the loop size in advance of attaching it to the bird, because a nightjar's wings are too long to be maneuvered into small loops. The loops were prepared with excess cotton thread forming much larger loops for easy mounting on the bird. When tied off, the loops were under very slight tension.

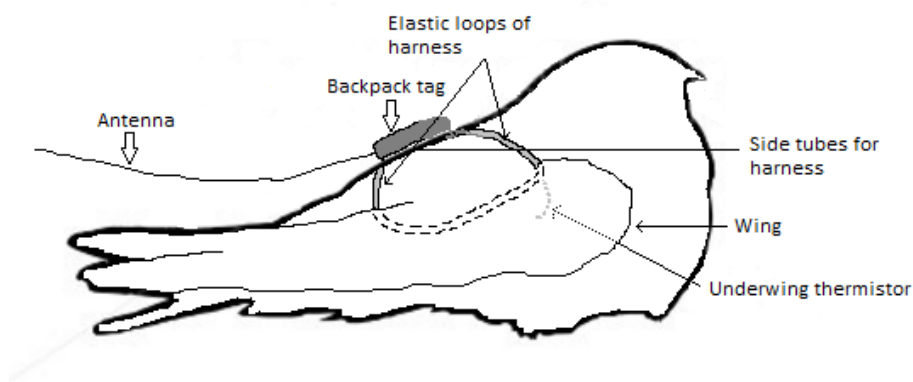


Figure 2.1. 2.0 g Biotrack TW-4/Ag39 backpack transmitter with underwing thermistor with side tubes to accommodate harness loops.

The weak link on half of the tags was formed by a single cotton thread, while on the other half the cotton was doubled. Two of the single cotton tags self-detached prematurely after 28 days, while at least one of the double cotton tags lasted 47 days (at which point the battery failed). The fate of two other tags was unknown, though the signal from the final single cotton tag was lost after 30 days. It is likely that the tag was shed at a feeding site outside the nesting area. The sixth tag (the first to be fitted) was removed from the bird after two weeks.

2.2.2.v Radio telemetry

Tagged nightjars were tracked from dusk until dawn between late-April and mid-August each breeding season 1994 and 1998. A focal bird was tracked each night, (although territory data were collected on other instrumented and noninstrumented birds in the vicinity) approximately every sixteen days, throughout the entire breeding season, resulting in ~6-7 nights of continuous data per bird. Birds were tracked when they became active at dusk (c. 21.45) until dawn (c. 04.50) with the last fix taken after the bird was stationary. Data were collected using burst sampling - while continuously monitoring the location of the bird - and taking a burst of locational fixes every 10 minutes. Such sampling results in locational data collected in short time intervals separating successive observations with comparatively longer time intervals between sampling bursts (Swihart and Slade 1997). Although only data on song territories is presented, the locations of foraging birds were also recorded and this resulted in over 250 fixes per bird which is above the recommended number of fixes required to accurately determine home ranges in other study organisms (e.g., Girard *et al.* 2002; Gitzen *et al.* 2006 but see Borger *et al.* 2006). Using this technique meant that we did not 'lose' the signal and therefore the nights' data but it allowed birds sufficient time to change location, ensuring independence of each fix (Kenward 2000). Signal range varied between 630 and 1,150 m depending on the terrain and proximity of 'shields' or obstructions that 'bounce' the signal. A single male regularly flew beyond these distances when foraging and terrain and signal bounce affected the accuracy of fixes.

To overcome problems of signal reflectance fixes were triangulated. This was done sequentially for each bird using compass bearings from each of three (sometimes two) locations recorded with a handheld GPS. To further enhance the accuracy of locational readings the antenna elements were held horizontally to provide a more accurate reading in wooded terrain (Kenward 2000). We also attached the antenna to a 3 meter hand-held pole and this helped give more precise locational readings in undulating ground. Instrumented birds could be located by a change in the frequency and volume of the

signal bleeps emitted by the receiver as the bird either changed direction while foraging or changed distance in relation to the observer. We were able to experimentally test the effects of flight pattern and distance to the signal characteristics by trialling a transmitter on a falconer's barn owl (*Tyto alba*) and this proved useful when tracking nightjars 'blindly'. We were able to distinguish three activity classes (Table 2.0) for each set of bearings and these were recorded along with time and other information about the location of the bird (e.g., type of song post).

Activity	Definition	% of fixes	~n fixes
Inactive	if the bird was stationary when all bearings were taken (this might have included 'active' behaviour, e.g., egg incubation or long bouts of inactivity between flycatching sallies)	61	4575
Active	if the bird was moving whilst one or more bearings were taken, this included hawking (continuous flight feeding), flycatching, flying between song posts, flying with mate, displaying or exchanging nesting duties, flying in a group, or chasing other birds and so on. The underwing thermistors were effective at accurately distinguishing between flying and flycatching	23	1725
Singing	if a male was churring during one or more bearing	16	1200

Table 2.0 Activity classes for radio tagged nightjars, percentage and number of fixes during which the activity occurred.

These broad activity patterns and relative percentage of activity were also recorded by Sharps (2013) when radio tracking nightjars so we can assume they are reliable for categorising behaviours. For each of the bearings, the 'known' activity was recorded within each category, e.g., active - displaying to female.

We aimed to triangulate 50% of fixes and collect two bearings for 50% fixes but this was dependent upon terrain, distance between fixes and activity of the instrumented bird. When birds were flying it was not always possible to gain two or more bearings and even when bearings were obtained they did not always overlap to produce an error polygon.

This occurred in 13% ($n \sim 975$) of fixes. In these circumstances we relied on visual sightings or calls as well as signal attributes to help us assign a bird to a particular habitat. If birds were on the boundary of two habitats we noted this as the fix and did not assign them to either habitat. We recorded the type of boundary because habitat boundaries appear to be important for nightjars when foraging. Particularly mobile birds were tracked using a mountain bike and occasionally a car. We attached the 3 meter pole holding the antenna to the frame of the bike in such a way as to allow the rider to rotate the pole and antenna. Except for one particular male birds rarely flew beyond the range of the receiver (i.e. the transmitter signal was lost briefly) and followed predictable routes. Birds sometimes visited more than one habitat during sampling periods, e.g., singing territory, tracks outside the territory and forest ride foraging sites.

To determine locational fix error we placed radio tags in various habitats (e.g., grass heath; bracken, clearfell, and conifer stock of different ages) because vegetation type significantly affects fix error (Garrott and White 1990). Tags were also placed at different heights (on the ground; horizontal log c50cm above the ground; 5m and 10m above the ground on deer seat) and attempted to locate them using triangulation at a distance comparable to the mean distance between triangulations used to locate tagged nightjars (see table 2.1).

2.2.3 Blood sampling

Blood samples are required for many types of ornithological research and a recent search on Google Scholar of the phrase 'avian blood sampling' returned 168,000 references. There is a growing body of research that has specifically focussed on this with the majority finding no effect of blood sampling on survival (e.g., Dufty 1988; Stangel and Lennartz 1988; Hoysak and Weatherhead 1991; Lubjuhn *et al.* 1998; Gaunt and Oring 1999, Schmoll *et al.* 2004, Perkins *et al.* 2004, Arnold *et al.* 2008), bird behaviour (Utter *et al.* 1971; Frederick 1986), or breeding success (Hoysak and Weatherhead 1991; Perkins *et al.* 2004; and Schmoll *et al.* 2004). There were no long-term effects from sampling small birds via

heart puncture, jugular vein, wing vein and venous occipital sinus (Stangel 1986). However, temporary weight loss was the main observed effect, and was particularly marked in house sparrows, (*Passer domesticus*). Mortality was also recorded but was attributed to overcrowding in the aviary and whether these findings can be generalised to wild birds is questionable (Stangel 1986). With regard to breeding behaviour a study on captive brown-headed cowbirds (*Molothrus ater*) and wild red-winged blackbirds (*Agelaius phoeniceus*) found no effect of brachial venipuncture. The study showed that male red-winged blackbirds maintained their territories, and females did not differ from the control group in terms of nest abandonment, nest success, and fledging rate (Hoysak & Weatherhead 1991). Finally, Ardern *et al.* (1993) assessed the effects of blood sampling on the behaviour of the endangered Chatham Island black robin, (*Petroica traversi*). They found that time-budgets for 20 birds (10 bled, 10 neither captured nor bled) were not significantly different, concluding that sampling had no adverse effects on behaviour. They continued to bleed a further 105 with only one accidental death.

However, the majority of studies that have found 'no effect' relied on recapture rates, i.e. within or between year, as their barometer for measuring evidence for no effect of blood sampling but this can be misleading. It does not take into account short term emigration from a study area or differences in detectability among groups of birds - i.e. 'trap-happy' verses 'trap-shy' birds (Brown and Brown 2009). Studies which rely on recapture percentage should measure the effect of blood sampling on annual survival probability, using birds only differing from the control by being bled. They should also factor in estimates of survival that control for potential differences in recapture rates among guilds of individuals (Lebreton *et al.* 1992). A long term ringing study found remarkably high reduction in survival rates for bled cliff swallows (*Petrochelidon pyrrhonota*) of 21-33 % depending on amount of blood taken and parasite-load but that these effects applied only in the year after sampling (Brown and Brown 2009). They argue that a blood volume of 1%-of-body-mass guideline may be too much. However, the American Ornithologists'

Union (1988) recommends that no more than 10-20% of blood volume be taken (1.5-2.5% of body weight) and see Gaunt and Oring (1999).

Finally, blood sampling can have species specific effects related to the relative amount of parental care and studies have yielded mixed results in terms of the impacts of blood sampling on birds. For example, mortality, return rates and clutch desertions varied in three species of wader. With regard to incubating and brooding behaviour, the biparental semipalmated sandpipers (*Calidris pusilla*) were more likely to desert their nests, when blood was taken from both adults, than when one or neither parent was bled. In contrast, desertion by uniparental phalaropes, red-necked (*Phalaropus lobatus*) and Wilson's (*Phalaropus tricolor*) was low, even when the attendant parent was bled (Colwell *et al.* 1988) (see Sheldon *et al.* 2008, Voss, Shutler and Werne, 2010 for a review).

2.2.3.i Blood sample collection

Blood samples were collected from 31 adult nightjars (20 male and 11 female) and 43 chicks (from 36 nests) in Nottinghamshire (1994-1995) and in 1998, 18 adults (12 male and 6 female) and 18 chicks (from 16 nests) in Dorset in order to determine the mating system and population structure of the nightjar. Adults were bled using brachial venipuncture and blood was taken from chicks using jugular venipuncture using a heparinised hypodermic needle and syringe. All blood volumes were less than the 1%-body-mass-volume recommended by Gaunt and Oring (1999). Samples were placed into eppendorf tubes containing either ethanol or DMSO and stored at -80°C until required. Blood samples were taken from chicks only when one or both of the suspected parents had previously been bled (to reduce unnecessary disturbance) meaning that 8 chicks from 5 nests were not bled. This reduced the amount of disturbance caused to chicks. In each of the nests, the larger (i.e. first chick to hatch) of the two chicks were bled first at ~13 days of age via jugular venipuncture. This date in the chick's growth was chosen for a number of reasons. Primarily, at this age the chick is well developed and the jugular vein is large and conspicuous. Secondly, the adult male tends to take over brooding the chicks at

about 15 days while the female incubates their second clutch (Cramp 1985). Because the chicks were weighed every fifth day from hatching, the third weighing session coincided with the male taking over brooding and he could thus be caught, without subsequent visits and associated disturbance. Thirdly, leaving it much later than this date might make it difficult to find the second chick to take a blood sample as the parents often move the chicks when the nest site has been disturbed (Cramp 1985). For comparison, in 1994, weight and wing length data were collected for both bled and un-bled siblings before, at, and after blood sampling. Data were collected when the brooding parent, usually the female, left the chicks to feed. At three nests on one evening no data were collected because the female did not leave the chicks or it was raining and at three nests sampled at 18 days the chicks 'exploded' (made a short flight into denser vegetation) and could not be measured.

Unlike the chicks, it is not feasible to catch the adults on repeated evenings to measure their body weight as this might cause undue distress and probably show very little. Furthermore, having a control group was not practicable due to the difficulty catching birds. Instead, immediate effects such as nest or territory abandonment were used to assess the effects of bleeding. The long-term effects of blood sample collection were measured using the rate of return of adult nightjars and breeding success.

2.2.3.ii Blood sample collection from nightjar chicks

The techniques involved holding the chick firmly in the left hand, such that the head pointed away from the body and the underside rested in the palm. Holding its legs between the ring and little fingers, and the head between the base of the middle and index fingers exposed the back of the chick's neck (illustrated in Hoysak and Weatherhead (1991)). The area was cleaned with a cotton swab soaked in absolute ethanol. This also allowed the moistened feathers to be groomed away from the vein. After gentle manipulations with the thumb of the same hand, and by gently pulling down on the right wing, the jugular vein rises to the surface of the skin. The syringe is held in the right hand

with the needle approaching the vein at an acute angle. Using the same thumb, or the bird's body, as a support for the needle, the needle was inserted through the skin, tip-up, by moving it slowly forward (Kerlin 1964). Once inside the skin, the vein was penetrated in a similar way. The skin and vein typically offered some resistance to the needle and care was taken not to push the needle in too rapidly. Once inside the vein, the needle was inserted to a depth of about 5mm. ~0.5ml of blood was obtained with ease by withdrawing the plunger with the tip of the thumb. Cotton wool was held over the insertion to accelerate the closing of the wound.

2.2.3.iii Blood sample collection from adult nightjars

Blood sample collection from adult nightjars was done by brachial venipuncture only. After catching the bird with a mist-net, it took two people to extract the blood. One person held the bird in a classic 'ringers-grip', with the bird on its back in the palm of the hand and its head between the base of the middle and index fingers, and the thumb across its abdomen. This calms the bird and reduces the chances of injury during blood extraction (Powell and Powell 1967). Nightjars open their bills wide when they feel threatened and make a loud hissing noise, while convulsing their body in an attempt to escape. This threat display was preceded by trembling, and an audible build-up of hissing, so the needle can be withdraw before the bird convulses. One of the bird's wings was stretched out to the side, allowing access to the axilla, where the brachial vein is situated (Baumel 1993). The area is cleaned with ethanol. In the axilla of nightjars the brachial vein passes over the humerus on the ventral surface, and although conspicuous, it is usually too narrow to attempt to take a blood sample without causing unnecessary damage to the surrounding tissue. Pressing on the heart-side of the vein increases its size by creating a temporary backlog of blood from the heart. After releasing the thumb it is a simple process of pricking the swollen vein, and drawing up the blood from the surface of the skin (Arctander 1988). The ethanol soaked cotton wool was held firmly over the puncture, helping prevent further blood loss. Using this method between ~0.5ml and 1m of blood was collected.

2.3 RESULTS

2.3.1 Fix Error

The mean distance for a sample of fixes was 168m, (n=100 fixes, ± 103 sd, range=22-1081m). This resulted in a fix error of 23m (± 18 m sd, range=2m-68m). We calculated the fix error for a small number (n=50) of nightjar locations and the mean was similar 27m (± 22 m sd, range=5-76m).

Habitat	Transmitter height	N fixes	Mean fix error
Grass dominated clearfell	Ground	10	12
	~50cm	10	2
Bracken dominated clearfell	Ground	10	19
	~50cm	10	14
<4 year plantations	Ground	10	17
	~50cm	5	26
	~10m	5	29
4-9 year plantations	Ground	10	25
	~50cm	5	68
	~5m	5	32
Heathland	Ground	10	15
	~50cm	10	5

Table 2.1. Mean location fix error for transmitters. Tags were placed at different heights - on the ground; horizontal log c50cm above the ground; 5m and 10m above the ground. On grass and bracken dominated clearfell, and heathland transmitters could only be placed on the 'ground' and '~50cm' above the ground. On <4 year plantations transmitters were located on the 'ground, ~50cm and ~10m' and in 4-9 year plantations on the 'ground, at ~50cm and ~5m'.

2.3.2 Effects of capture techniques

2.3.2.i Mist netting

Using vertical mist netting and a tale lure (commercial recording of a UK nightjar) 67 male, 15 female, and 20 juvenile nightjars were caught over four seasons, 1994-1997 (Nottinghamshire) and 19 male, 11 female and 6 juvenile nightjars were caught in 1998 (Dorset), resulting in an 81% success rate for catching attempts. In 38% and 53% of

captures the bird was trapped in the first and second pocket (from the bottom) of the mist-net respectively, while the majority of the remainder were trapped in the third. Females also responded to the tape recording of the singing male nightjar. During the investigations reported below, five mated females flew over a kilometre, beyond the boundary of their own mate's territories, in response to the tape recorder and were caught immediately. These birds are likely to have been foraging or may have been seeking extra pair copulations.

There was no evidence of capture myopathy; i.e. the birds flew directly after being released but see section 2.3.3.i. Regrettably, one juvenile bird (Nottingham) strained a wing during extraction from the net and subsequently died 10 days later in the care of a local veterinary. Although the wing had healed the bird would not feed.

2.3.2.ii Flush into static net

Eight females and 2 males (Nottingham) and 3 females (Dorset) were captured in this way. There were no recorded injuries and none deserted their nest. Based upon number of catching attempts this method had a 90% success rate and there were no injuries or mortalities.

2.3.2.iii Drop netting (horizontal mist netting)

Four females and 1 male (Nottingham) were caught while brooding chicks using this technique. There were no incidents of nest desertion, injury or mortality using this technique. This was a less desirable capture technique than vertical mist-netting for two reasons. First, it was only 50% (based on catching attempts) successful and therefore not as effective as the above techniques, and second, we considered it more stressful for the bird.

2.3.3 Effects of tail-mounted radio tags on adult male nightjars

2.3.3.i General effects

Anecdotal evidence from observations on the behaviours (i.e. activities such as churring and feeding) of ~20 instrumented and non-instrumented birds shows that all initially remained inactive after being released, often remaining motionless where they had been released (e.g., roof of car) and did not fly unless they were encouraged. Males typically (~90%) did not chur and their feeding activity was suppressed. However, by the following dawn, or at the latest the following evening, the birds appeared to be engaged in 'normal' activity.

2.3.3.ii Breeding success

In both studies the fecundity (measured as fledglings per breeding attempt (FPBA) at 18 days from hatching) of instrumented and non-instrumented birds was compared. In Nottinghamshire (1994), the overall breeding success for the forest was 1.24 FPBA based on 21 nests. FPBA for 1992 (based on 22 nests), 1995, (19 nests), 1996 (22 nests) and 1997 (23 nests) was 1.23, 1.16, 1.32 and 1.17 respectively for untagged birds only (Table 2.2). Comparison between tagged and untagged birds in 1994 showed similar success rates with 1.33 chicks per nesting attempt (based on 12 nests) and 1.11 chicks per nesting attempt (9 nests) respectively. In Dorset, comparison between tagged (not including backpack transmitters) and untagged birds shows that tagged birds had a nesting success of 1.16 FPBA (based upon 6 nests) compared to 1.25 for non-instrumented birds (based upon 8 nests). Two nests of instrumented birds were predated at the egg stage and 1 chick died before fledging and 2 nests of untagged birds were predated at the egg stage. One instrumented female was tracked to her nest and subsequently flushed exposing one egg. We revisited the nest site 5 days later but the female had moved leaving the egg. She had a second successful breeding attempt ~1.1 km from the failed nest within the territory of a different male.

Year	1992	1994 † *	1995*	1996	1997	1998 † *	Total Tagged	Total non-tagged
Nests (n)	22	9(12)	19	22	23	8(6) {3}	21	103
Fledgling (n)	27	10(16)	22	29	27	10(7) {4}	27	125
FPBA	1.23	1.11(1.33)	1.16	1.32	1.23	1.25(1.17) {1.33}	1.29	1.21

Table 2.2 Between season FPBA of tagged † and bled* nightjars compared to control birds breeding in Sherwood Pines Forest Park, Nottinghamshire (1992-1997) and Wareham Forest, Dorset (1998). Numbers in () represent tagged birds and numbers in {} represent backpack birds. Breeding data for 1992 and additional breeding data for 1994 – 1997 was provided by J. Stoner.

2.3.3.iii Recapture rate and philopatry

With regard to re-occupancy of territories by returning adults in subsequent breeding seasons, data is available from 1992 to 1997 for Nottinghamshire only (Table 2.3). Only one bird displayed nest site fidelity between 1992 and 1997 (except 1993). It should be noted that these comparisons are based upon very small samples but philopatry is similarly low for instrumented and noninstrumented birds.

Year	Number of retraps		Total	Nest site fidelity
	Tagged or Bled	Control		
1992	na	3	3	1
1993	na	2	2	0
1994	na	4	4	1
1995	3	1	4	1
1996	2	1	3	1
1997	2	2	4	1

Table 2.3. Number of tagged and bled nightjars and controls caught in Sherwood Pines Forest Park (1992-1997) that re-occupied their territory. Retraps were caught within 1km of the location where they had been caught in previous years except for 1 male caught 3km further west.

2.3.4 Effects of harness (backpack) radio transmitters on adult nightjars

2.3.4.i Physical signs of damage caused by tagging

Initially only one male nightjar was fitted with the harness radio tag that had a mate incubating 2 eggs. The instrumented bird was tracked each evening for the following week

and despite catching attempts, it was not re-caught for two weeks. There were no visible signs of abrasion to the feathers or skin of the nightjar and his female was still incubating. This is despite the fact that the loop elastic stretched and had become loose. Using different elastic and marginally tighter loops refined the design. The improved design was fitted to five more birds.

As this was a novel application of the harness radio tag all the instrumented birds were monitored closely. One of the five birds fitted with the improved harness design was re-trapped the evening after it lost its tag (and 22 days after the initial tag attachment date). It was examined carefully for signs of damage caused by the tag. There was some loss of feathers (~20%) in a 2 cm band across the centre of the back. Examination of the under-wing revealed minor feather loss (~5%). There was no discernible damage to the skin on the bird's back, nor on the leading edge of the wing. The bird was 2 g heavier (after allowing for the weight of the tag) than it was when the tag was first fitted.

2.3.4.ii Breeding success

We compared the fecundity of focal birds post instrumentation, with nine birds that had tail-mounted radio tags fitted a week or so before and non-instrumented birds breeding in the same forest. With regard to breeding success rate, the FPBA for non-instrumented birds in the Wareham Forest study was 1.25 (Table 2.2). A comparison between birds' wearing backpack tags and non-instrumented birds showed the backpack wearing birds to have the highest FPBA with 1.33 fledglings (based on three nests) and the non-instrumented birds produced 1.25 fledglings (based on eight nests). All the mortalities occurred during incubation and were caused by predation, except for a brood of c6 day old chicks that were predated.

2.3.5 Effects of blood sample collection

2.3.5.i Growth rates and mortality of nightjar chicks

No mortality was directly attributable to this sampling technique. The most obvious signs of injury were bruising caused by the entry of the needle and minor bleeding post blood sample collection. A more serious short-term effect was the lack of increase in weight from the sampling evening in 17 out of 19 chicks (Figure 2.1). A general linear model with repeated measures found a significant difference in mean weight gain between the two groups ($F=48.5$, $df=1$, $p<0.001$). Indeed, these chicks actually lost a mean weight of 1.35g. Overall, their daily mean increase in weight was 2.65g. The smaller chicks in the brood that had not been bled increased their body mass by a mean of 2.83g per day. Blood sample collection may have caused a lethargic reaction in the chicks. Also, pain and stiffness in the neck may have inhibited the chicks' begging behaviour.

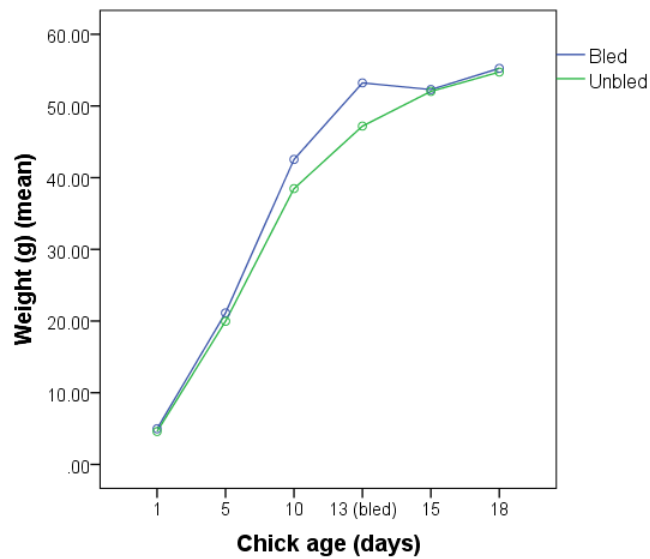


Figure 2.1. Comparison between the change in mean weight (g) at 1, 5, 10, 13, 15 and 18 days after hatching for bled versus non-bled chicks. The scale on the x-axis is not equal to the time interval. Error bars are not fitted because standard errors were so minor. Bled chicks are heavier prior to bleeding because the larger chick was bled in each nest.

In one nest, the unbled sibling was found dead and the bled chick had lost 3.1 g 5 days after being bled. The evening it was bled it only weighed 44.4 g compared to the mean weight of its cohort which was 53.18 g. The large black slug *Maximus* was eating the

faeces from the rear of chick two, and another was apparently feeding on the dead chick. Even though the adults were flushed nearby, it appeared that the presence of the slugs might be keeping them from brooding. Two days later, the surviving chick was also found dead, some two meters from the original nest site. The corpse was very fresh, and although rather academic, measurement of its weight revealed that it had gained 0.7 g. Cause of death was difficult to ascertain but the death of its sibling and its generally retarded development implied some form of illness, possibly parasitic.

The mean daily increase in weight of bled nightjar chicks compared to non-bled siblings was 2.65 g and 2.83 g respectively (Figure 2.1). Both figures are lower than those recorded by Berry & Bibby (1981) for chicks reared at Minsmere, Suffolk. They also showed a mainly linear growth rate at 4.48g/day for the first ten days and a stabilisation at 50-60g thereafter. The growth rate of the control chicks in this study rose from 2.86g/day between 1 and 5 days to 3.95 g/day between 5 and 10 days. The bled chicks' weights increased by 3.35g per day between 1 to 5 days, and by 4.24g per day between 5 and 10 days. After bleeding, weight increase fell to 1.36g/day compared with 2.66g/day for non-bled chicks.

2.3.5.ii Wing growth

Wing length growth showed no evidence of difference between bled and control chicks and continued at a similar, linear mean rate of 6.37mm per day, compared to a mean rate of 6.35 mm per day for the control group (Figure 2.2). This was lower than the findings of a study by the SRG (1982), which was 6.75mm per day, and remained almost linear. Between 1 and 5 days mean growth was 5.31 mm/day but increased to 6.85 mm/day between 10 and 15 days. The SRG (1982) noted that after fledging wing growth levelled off producing a sigmoidal curve. Although, a general linear model with repeated measures found a significant difference in the mean increase in wing length between the two groups ($F=15.125$, $df=1$, $p<0.001$) this was attributed to the very small variations in the standard error. Wing length growth in the chick that died was well below the mean for the other

bled chicks and was 86 mm compared to a mean of 92 mm on the evening it was bled. Measurement of the corpse showed a wing length of 91 mm.

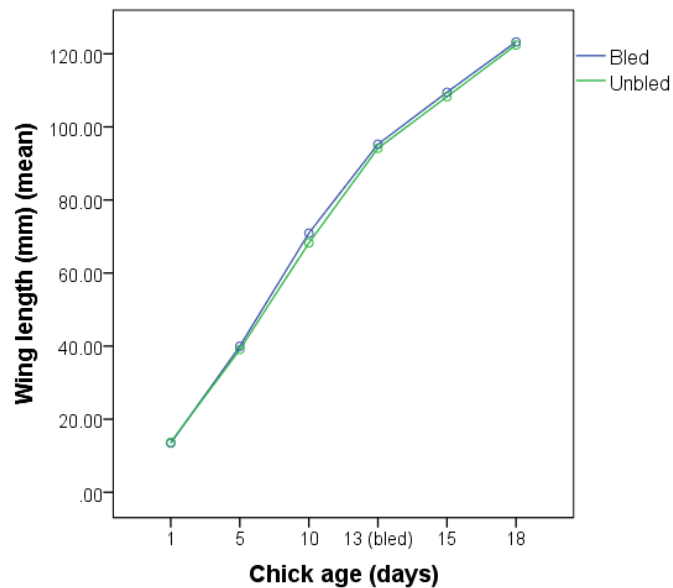


Figure 2.2. Comparison between the change in wing length (mm) at 1, 5, 10, 13, 15 and 18 days after hatching for bled versus non-bled chicks. The scale on the x-axis is not equal to the time interval.

Late on in the seasons of 1994 and 1995, seven of the bled chicks were caught as juveniles in mist nests. Both their mass and wing lengths were comparable to non-bled juveniles caught during the same period. Mean wing length was 189.3mm (n=7, sd=1.86mm - bled birds) compared to mean of 187.6mm, (n=4, sd=2.43mm). Mean weight was 78.25g (sd=4.34g) for bled juveniles compared to mean weight of 75.8g (5.13g) for four non-bled juveniles. Juveniles cannot be sexed reliably.

2.3.5.iv Behaviour of adult nightjars

None of the sampled birds abandoned their eggs or chicks, and males continued to defend the same area of territory post-bleeding. Their breeding success was comparable to those of previous and subsequent breeding seasons (table 2.2) (Anova, $F=0.083$, $df=8$, $n=124$, $p=0.999$).

2.4. DISCUSSION

This study set out to determine the effects of researcher activity on the welfare and breeding success of two populations of nightjars breeding in lowland pine plantations. Tape luring into a static mist net is the most effective way of catching male nightjars. To catch brooding females, the approach of flushing her into a static net was successful and caused minimal disturbance to the nest area. In the minority of cases, lowering the net onto a brooding adult was the only feasible capture technique. None of the birds in this study showed signs of capture myopathy or abandoned their nests or territories after capture.

There were no measurable long-effects on breeding success or philopatry of nightjars in terms of radio tagging and tracking although a tagged-female abandoned a single egg after being tracked to and flushed from her nest site. Short-term effects included premature loss of the central rectrice and small amounts of feather wear beneath the backpack transmitter of instrumented birds. FPBA was similar for instrumented birds compared with non-instrumented birds nesting in the same forests.

With regard to blood sample collection, only immediate effects such as bruising and lethargy were recorded for the focal birds. The bled chicks also experienced a brief reduction in weight, and slower weight gain than non-bled siblings (Figure 2.1). A bled chick died along with its sibling and neither chick gained weight at similar rates to the other chicks in the study. Bleeding had no effect on wing growth rates (Figure 2.2). Adult nightjars experienced no measurable long-term effects from bleeding, and after an evening of relative inactivity, they behaved normally, with a comparable breeding success to non-bled birds from previous and subsequent breeding seasons (Table 2.2), and comparable return rates in subsequent breeding seasons (Table 2.3).

2.4.1. Capture

Mist-netting is the most effective and least obtrusive way of catching both adult male and female nightjars (Squire & Alexander 1981). In this study, no birds abandoned their nest or territory after capture, unlike a study by SRG (1984), and no chicks were trampled (BRG 1992), and personal communication with other nightjar fieldworkers (Cresswell; Alexander; BRG) helped formulate a best practice procedure for capture of nightjars at different breeding stages. One fatality was directly attributable to mist netting. A juvenile suffered capture myopathy (Williams & Thorne 1996, Marco *et al.* 2006, Ruder *et al.* 2012), apparently straining either the large appendicular muscles or a wing during extraction from the mist net. Once in the care of a veterinary, the damaged tissue apparently healed, but the bird would not eat and died. The mortality rate of 0.75% is below the 1% target specified in Ralph *et al.* (1993) and is within the range reported for other species, e.g., 0.6% in Kenyan forest species caused by predation (Brooks 2000) and 0.5% in Australian heathland birds and 2.8% in forest species also due to predation and handling (Recher, Gowing and Armstrong 1985).

To the author's knowledge very few studies have considered the effects of drop-netting (Bub 1991) (horizontal mist-netting) on ground nesting birds with studies reporting only its use (e.g., Bacon and Evrard 1990, Stokes, Stokes and Schultz 1995). Aruch, Pratt and Vetter (2003) found that drop netting Kalij pheasants (*Lophura leucomelanos*) was less effective than using open-door or box traps and resulted in one minor injury (based on 5 birds) . Although this study found no evidence of nest desertion anecdotally it appears more stressful for the birds because it is able to make more attempts to escape before it is caught and disturbance occurs at the nest site. Furthermore it was only 50% successful and therefore not as effective as vertical mist netting.

2.4.2. Tagging

Tail-mounted radio-tagging has been performed on nightjars for over three decades and although few effects have been observed, to the author's knowledge, no systematic

research has been done to quantify them. This study is consistent with the findings of the Stour Ringing Group (1982-present), Alexander & Cresswell (1990) and Bowden & Green (1991) that there are no measurable effects of instrumentation on behaviour or breeding success (Table 2.2). Both Alexander and Cresswell (1990) and Bowden and Green (1991) fitted tail-mounted radio tags to nightjars. The latter radio tagged 29 birds (17 male and 12 female) nesting on the forestry plantations of Thetford Forest, in East Anglia with 'no reported effects on the nightjars' breeding ability'. The breeding success of the birds in the 1994 Nottinghamshire study was 1.33 FPBA attempt (based on 12 nests), compared with 1.11 FPBA for non-instrumented individuals (based on 9 nests), and in the Dorset study, the breeding success of the nine tail-mounted transmitter wearing birds was 1.66 (based on six nests) and the non-instrumented birds produced 1.13 chicks (based on eight nests), thus supporting their observations. Alexander and Cresswell have been instrumenting nightjars since 1982. The only measurable effect of fitting the radio tag was the premature loss of the central rectrice housing the radio-transmitter (pers. comm. Cresswell). This was also recorded in this study and as this is the first tail feather to be shed during moult (Cleere 1998) the effects on the bird should be minimal. However, we did flush a radio tagged female from her nest site which she abandoned leaving a single egg. Females are more likely to desert their nest site (location chosen by pair for egg deposition) once disturbed if they have no eggs or a single egg (Cresswell pers. comm) and this has implications for nest finding in general. Post-instrumentation, birds should be allowed sufficient time, ~7 days to establish their nest, free from human disturbance, before attempts are made to locate the nest. This depends on the breeding stage wherein the effects of disturbance will be more marked during nest establishment and initial egg laying. Other researchers including Sharps *et al.* (2015) and Cross *et al.* (2005) also used tail mounted tags with no reported effects.

Studies on other species have shown varying results. For example, nest attendance reduced in instrumented versus noninstrumented sooty shearwaters (*Puffinus griseus*) (Sohle *et al.* 2000) and instrumented females were more likely to cease incubation and

brooding (Hedd *et al.* 2001). Although reduced breeding success was not recorded for nightjars there may be effects that this study did not detect. For example, compensatory-preening might negatively affect vigilance, foraging effort or parental care (Hirons and Owen 1982, Barron *et al.* 2010) or indirectly affect the fitness of non-instrumented mates who make up the shortfall in provisioning by instrumented mates (Paredes *et al.* 2005). Casas *et al.* (2015) found significantly higher mortality (15%) during the first week after capture than during the following weeks (< 2.5%) in pin-tailed sandgrouse (*Pterocles alchata*), and this increased with relative transmitter and harness weight, and handling time.

Back-pack tags were used on nightjars for the first time. No prolonged effects were observed with regard to changes in behaviour, such as excessive preening but incidences of this would be difficult to observe in nocturnal species (Robert *et al.* 2006), nor were there any observable physical effects on the birds such as weight loss (nightjars gained weight) as was found in a study by Perry (1981) on the north American duck, the canvasback (*Aythya valisineria*). However the sampling method might not have detected weight loss directly after tagging as birds were not caught and re-weighted until 2-3 weeks after instrumentation. Only minor physical damage to the skin and feathers immediately beneath the tag was observed, and was recorded in Greenwood and Sargeant's (1973) study on captive mallards (*Anas platyrhynchos*) and blue-winged teal (*Anas discors*) and Hines and Zwickle's (1985) study on juvenile grouse. Effects of tagging are likely to affect species differently based upon life history and ecology and results might not therefore be generalisable.

The degree of philopatry demonstrated by nightjars within the forest may give a more sensitive measure of the effects of tagging. A comparison of the recapture rates of instrumented and noninstrumented birds between breeding seasons showed that site fidelity (i.e. re-occupancy of territory) was equivocal between the two groups. In 1995, 1996, and 1997 retraps of formerly instrumented males was slightly higher than non-

instrumented birds from the previous season but the numbers are very low (Table 2.3). The return rates and re-occupancy of territories in subsequent breeding seasons showed ratios of 3:1, 2:1 and 2:2 for formerly instrumented and noninstrumented males respectively for 1995, 1996 and 1997. Recapture rates might be biased by the age or sex of the bird. For example, Roche *et al.* (2013) found that experienced birds (i.e. those caught at specific locations in previous years) were able to avoid capture and if this also applies to nightjars the results are encouraging.

Although the sample size was small, the period over which the experiment was carried out was short, and birds were instrumented at different stages of breeding, it seems likely that the trauma caused by trapping and handling has the most obvious, but short term effect on the instrumented bird, and that the radio transmitters might cause only minimal discomfort.

2.4.3. Blood sampling

The effects of blood sample collection on focal species has become the focus of a growing number of studies, (e.g., Colwell, *et al.* 1988; Duffy 1988; Hoysak & Weatherhead 1991, Brown and Brown 2009) and reviews (e.g., Sheldon *et al.* 2008, Voss *et al.* 2010), with only one study focussing on aerial insectivores (Brown and Brown 2009). In this study, chick development was affected in terms of short term weight loss but there was no measurable effect on wing growth. Such transient effects were found in starling (*Sturnus vulgaris*) chicks wherein jugular venipuncture had no effect on wing growth but resulted in short term weight loss during the first week after hatching, but this effect disappeared by the second week (Sheldon *et al.* 2008). The slowing in weight gain after 10 days is consistent with Berry & Bibby (1981) but is clearly more marked for the chicks bled at 13 days. Temporary weight loss was also reported in house sparrows (*Passer domesticus*) that had undergone jugular venipuncture (Stangel 1986).

After bleeding, growth remained linear to non-bled chicks and there was a non-significant difference in growth rate between bled and non-bled chicks. A single bled chick died, probably due to infestation, and exhibited a retarded wing growth rate. This is consistent with findings by SRG (1982) that showed disease, lack of food and exposure to low temperatures and precipitation caused a reduction in wing growth rates of nightjar chicks in Wareham Forest, Dorset, before the birds died.

Such continued handling (without bleeding) had 2 long term effects on nightjar nestlings. Firstly, nestlings were smaller than they would have been if they had not been bled and secondly they will have taken longer to reach their maximum weight. A study on the long term effect jugular venipuncture on chick development and nest success in dickcissel (*Spiza americana*) found no such effect (Monroe *et al.* 2014), but it appears that both body mass, but less so wing length growth rate of nightjar chicks are sensitive measures of fitness and that bleeding appears to have both immediate and lasting effects. However, the weight of the extracted blood will have reduced the weight of the bled chicks and should be factored into measures of weight loss (~0.5 mls, with an approximate weight of 0.5g, was taken).

Adult nightjars experienced similar breeding success to non-bled birds breeding in the same forest. This is not supported by studies by Colwell *et al.* (1988) who showed that the bi-parental semipalmated sandpiper (*Calidris pusilla*) in their study deserted their nests post bleeding when both adults were bled, whereas the paternal phalaropes didn't. Shorebirds however have very different ecologies to nightjars. In this study none of the bled birds deserted their territory and this is supported by Hoysak & Weatherhead (1991) who showed that male red-winged blackbirds (*Agelaius phoeniceus*) maintained their territories after bleeding and that bled females did not differ from the control group in terms of nest abandonment, nest success, and fledging rate. Finally, annual return rates were comparable to those of non-bled birds but number of recaptures are very low (Table 2.3). Despite the fact the nightjars are philopatric, return rates (i.e. the number of

returning birds caught on their breeding grounds the following season) is very low, because juvenile mortality on migration is estimated at 75% (Cramp 1985). However, in 1996, BRG caught 2 of the juveniles that were bled in 1994. This is a reassuring result because one might anticipate that bled birds will be more likely to disperse post bleeding or become wary of recapture (Voss *et al.* 2010, Shutler and Clarke 2003) and therefore reduce the likelihood of recapture. However, as Brown and Brown (2009) point out, birds that were caught for instrumentation might be 'trap-happy' and one would expect to catch them again suggesting that if one does not they may well have died.

Evidence for long-term effects of blood sampling was not recorded by Angelier, Weimerskirch and Chastel (2011) when studying return rates for black-browed albatrosses (*Thalassarche melanophris*). However, Brown and Brown (2009) found that annual survival of bled cliff swallows (*Petrochelidon pyrrhonota*) was lower than that of non-bled birds, with bled birds experiencing a 21-33% reduction in average survivorship. Their results suggest that brachial blood sampling is not a benign technique and that the blood volume taken should be less than 1% of the body mass. However, they found that repeated sampling had the greatest effect on survivorship.

It appears that careful blood sampling does not cause mortality. This may be because nightjars (and birds more generally) do not exhibit acidosis and thus do not go into shock when blood is lost (Sturkie 1986), and that birds in general can recover from relatively greater blood loss than mammals (Kovach *et al.* 1969). This and other studies demonstrate that blood sampling can be performed without causing mortality or long term interference with the behaviour, reproductive success and survival of bled individuals (Ardern *et al.* 1993). Evidence of adverse effects to some individuals may have been caused by the capture techniques and prolonged handling. Such capture myopathy may have caused the deaths of the waders in Colwell's *et al.* (1988) study. However, some studies did show that effects of sampling varied between species (Sheldon *et al.* 2008) with different parental care, e.g., Colwell (1988). Others guard against sampling during migration periods (Duffy

1988) and therefore, it is pertinent to tailor studies that involve blood sampling to the species under investigation. Indeed, blood samples can be collected from plucked feathers negating the need to collect blood intravenously (Harvey *et al.* 2006).

In conclusion, tagging, and to a greater extent blood sampling, have been shown to have immediate and longer term effects on nightjars but the advent of modern molecular and telemetry techniques means that blood sampling and intensively following instrumented birds are no longer necessary. Therefore best practice recommendations for tagging and blood sampling are no longer required. By using gps transmitters researchers can remotely monitor the movements of instrumented birds thereby minimising disturbance during critical times in the birds breeding cycle. For studies that require DNA researchers can collect feathers from birds, or from nest and roost sites without the need to capture birds.

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CHAPTER THREE

HABITAT SELECTION FOR SONG TERRITORIES BY THE NIGHTJAR *CAPRIMULGUS EUROPAEUS* NESTING IN LOWLAND PINE PLANTATIONS

Abstract

Determining bird territories using territory mapping and radio telemetry is commonplace in censusing bird populations, but each method has their limitations when used alone. Potential limitations of territory mapping are territory overlap and counting of unmated males. Radio telemetry is time consuming and involves close contact with the organism. Both territory mapping and radio telemetry were used to determine habitat selection for nesting. Attributes of song territories were measured and included; area, compactness ratio (i.e. circularity of territory where 1 = perfect circle), distance of nest site to habitat boundary, type of boundary, vegetation height and density around the nest site. Habitat selectivity for nest sites was measured by comparing nightjar nests to randomly stratified sample (nest) sites in unoccupied but similar habitat determined using random number tables. Behaviour of radio tagged male nightjars reveals that their breeding status can be established without finding their nest site and that mated and unmated males had similar territory attributes for area (mated mean 7.1 ha, unmated mean 8.37 ha,) but territories were significantly less compact for unmated territory holders - (mated mean=0.66, unmated mean=0.57). Territory overlap was as high as 80%. Nightjars are conservative in their habitat choice and defend a breeding territory but do not defend foraging areas. Nightjars nested in 4 broad habitat categories, clearfell, <4 year plantations, 4-9 year plantations and heathland. Territories and nests sites of mated males in the different habitats were significantly different for area, breeding density and vegetation height and cover surrounding the nest. Compared to randomly chosen nests nightjars nest closer to soft edges (gradual height transition between contiguous habitat), avoided nesting adjacent to hard edges (rapid height transition between contiguous habitat) and nested in vegetation of intermediate density to the range available. It appears that nightjars avoid hard edges possibly because they provide elevated perches for predators and require a balance between nest concealment and vigilance and that predator avoidance might be an important factor in nest site choice. Two potential issues arise when using territory mapping for national nightjar surveys: the similarity of the territories of mated and unmated males' and not accounting for territory overlap. Counting all singing males leads to population overestimates and not being aware of territory overlap leads to underestimates so these should be taken into consideration when interpreting census data.

3.1 INTRODUCTION

This chapter is twinned with Chapter Four. The focus of this Chapter is to provide a detailed description of habitat selection by two populations of nightjars nesting in lowland pine plantations. Chapter Four uses this information to measure the effects of habitat selection and researcher activity on nest predation rates and nest survival using a comparison between nightjar and artificial nests.

The nightjar has experienced a significant and long term decline in numbers and in range throughout the second half of the 20th century, primarily due to habitat loss and is subsequently a Species of European Conservation Concern (SPEC2) (Birdlife International 2004) and is protected under Annex 1 of the EU 'Birds' Directive (EC 1992). The loss and fragmentation of its 'normal' breeding habitat, heathland, has meant that other, semi-natural successional habitats have become important, and none more so than commercial pine plantations. The 2004 population census by Conway *et al.* (2007) found that 57% of the UK population occurred on forest plantations but in such habitats, and in particular heathland patches, nightjars are susceptible to nest failure due to recreational disturbance (e.g., Lowe *et al.* 2014). Therefore, this study sets out to understand how nightjars use commercial plantations for nesting and to use this information to design the study in Chapter Four, which uses artificial nests to measure the effects of habitat selection and disturbance on nest predation.

I start with a review of causes of avian habitat selection, and then describe field studies of site usage in the nightjar.

3.1.1. Habitat selection: song territory and nest site

Long established theories on habitat selection in birds including MacArthur (1958, 1972), and Holmes *et al.* (1979) stated that bird communities are organised by competition for food. MacArthur (1972) and others showed that avian assemblages increase with

increased vegetation density and spatial heterogeneity. The basis of these assumptions are rooted in the argument that birds choose habitats with greater foliage density because it supports more food, thus greater structural heterogeneity may accommodate the differential foraging requirements of different species and thereby reduce competition. Furthermore, many authors have concluded that birds defend large territories when they utilise them for feeding (e.g., Stenger 1958 but see Lack 1954; Hinde 1958 and Brown 1964) and large bodied predatory species defend the largest territories (e.g., Schoener 1968; Ottaviani *et al.* 2006). However, the nocturnal foraging niche occupied by nightjars (and lack of competition with diurnal species) coupled with observations that nightjars commute variable distances (e.g., mean distance 3.1km, range <1km - 6km in Alexander & Cresswell 1991) to foraging areas (Bowden and Green 1991; Kenyon 1998; Cross *et al.* 2005; and Larsen 1994 and 1998 unpub. data) suggests other explanations for habitat selection in this species.

One of the most important selective factors shaping avian life histories is nest predation (Lima 2009), and therefore other hypotheses, such as predator avoidance, may be important in habitat selection (Newton 1998; Willson *et al.* 2001; Whittingham and Evans 2004; Ibanez-Alamo *et al.* 2015). For example, studies have shown that birds alter territory establishment and nest site choice when predators are removed (Fontaine and Martin 2006), and when experimental changes in habitat reduce predation risk (LaManna *et al.* 2015). Birds then reduce predation through specific nesting associations and this affects both habitat choice and nesting density (reviewed by Quinn and Ueta 2008). For example, a study by Richardson & Bolen (1999), reported that bullock's orioles (*Icterus galbula bullockii*), nested in aggregates around yellow-billed magpie (*Pica nuttalli*), nests, and had greater breeding success afforded by the nest defence of the magpies, than oriole nests not associated with magpie nests. The relative importance of protector species and their impact on territory and nest site selection is probably underestimated, and might be important for species conservation (Fletcher 2008).

Natal philopatry and breeding site fidelity have been shown to be important determinants of habitat selection in birds (Hilden 1965, Greenwood 1980, Greig-Smith 1982). There are different theories regarding the evolutionary basis for natal philopatry and these will not be reviewed here but in simple terms some avian species might benefit from inbreeding (Sheilds 1982) or outbreeding (Weatherhead *et al.* 1994) and in particular that migratory species would benefit from returning to the same locality to increase their chances of finding a mate (Weatherhead *et al.* 1994), especially if that habitat was scarce. Familiarity with a breeding site, especially a successful one, will benefit individuals (Piper 2011) who may develop a cumulative knowledge (memory of breeding success) and return (Schmidt and Whelan 2010). It is however important to consider habitat selection at the population level. Density dependent effects will be more marked when populations are dense and individuals may be forced to occupy atypical and unsuitable habitat (e.g., pied flycatchers (*Ficedula hypoleuca*) Alatalo *et al.* 1985), whereas when the population density is low (e.g., in degraded habitats) individuals may be more likely to exhibit greater bias for good territories/nests sites (Schmidt *et al.* 2015).

Birds also use natural cues to detect the presence of predators and adjust their territory and nest site choice accordingly. For example, ground-nesting passerines eavesdrop on calls of Chipmunks (*Tamias striatus*), lowering nest densities near playback sites (Emmering and Schmidt 2011). Passerines and ducks avoided establishing territories in areas experimentally treated with nest predator urine and faeces (Eichholz *et al.* 2012; Forsman *et al.* 2013).

Birds establishing territories and nest sites might rely on the presence of con/heterospecifics as indicators of habitat 'safety' (Thompson 2013) and arriving on breeding grounds slightly later might allow them to make more optimal choice of territory and nest site in terms of predator avoidance (Loukola *et al.* 2012) but not necessarily the best territory from other perspectives.

Numerous density dependent factors (not related to predation) also govern habitat selection in birds. For example, likelihood of cuckoldry increases in colonial species or in individuals within species with small territories (e.g., Moller and Birkhead 1992, but see Westneat and Sherman 1997) and therefore a large territory early in the breeding season may reduce the occurrence of extra-pair fertilisations (EPF). Territories may decrease in size after a mate is incubating and EPFs are less likely.

Habitat selection (and territory size) may act as an indicator of male quality (e.g., Seddon *et al.* 2004). Larger territories may contain more alternative nests sites which may be required after a failed breeding attempt. Though female mate choice may affect territory attributes (Alatalo *et al.* 1986), many authors agree that territory quality may be strongly positively correlated with male quality and experience. This should affect the quality and the size of breeding territories because of differences in resource holding power of individuals (Moller 1988).

Numerous other landscape effects, functioning at varying spatial scales, influence habitat selection in birds including, habitat loss (e.g., Dolman and Sutherland 1995), fragmentation (e.g., Wilcove 1985; Wilcove, McLellan and Dobson 1986), and human disturbance (e.g., Miller, Knight and Miller, 1998). Dispersal distance has also been shown to affect territory size (e.g., Bowman 2003).

Microhabitat might also affect nest site choice due to its influence over microclimate. Such environmental factors in ground nesting birds may include the thermal properties of the substrate. These include rates of nightly temperature radiation, and daily insolation. Nocturnal cold stress is one of the most studied aspects of microclimate effects of nest site choice (Cody 1985). Many authors have concluded that the effects of nest site choice upon nightly radiation are substantial (Balda & Bateman 1973; Calder 1973). However, studies that have generated thermal budgets are largely restricted to diurnal species (reviewed by Prinzinger, Pressmar and Schleucher, 1991). They have focused on how nest

site choice and design reduce temperature loss during the night (as well as controlling insolation during the day). Nocturnal temperature loss may present nightjars with an even greater problem of keeping their eggs/chicks warm during the evening, while meeting their energy requirements and maximising insolation during the day might therefore be important (Tate 1989).

Birds do not simply nest in the densest vegetation available to them (Cody 1985). Predation is not then solely related to degree of concealment (e.g., Burhans & Thompson 1998, Braden 1999) due to a trade-off between nest crypsis and the requirement for prey species to see predators (e.g., Gotmark *et al.* 1995; Cresswell 1997). Both concealment and the physical barrier afforded by dense vegetation may increase fitness and predator avoidance may be the selective pressure by which individuals distribute themselves (Camp *et al.* 2013). Thus, predation and nest site choice may be linked with foliage density, whereby birds chose to nest in the structurally most heterogeneous vegetation (Martin 1993). For this to be the case Martin (1993) proposed the total-foliage hypothesis, which states that prey achieve a reduction in predation with increased foliage density because of the increased levels of concealment and consequent reduced transmission of biological cues. Dense vegetation not only provides greater concealment, but more potential nest sites, and therein more potential prey sites which a predator has to search in order to encounter prey. Martin (1993) called this the potential-prey-sites hypothesis and we will test this by counting the number of alternative nest sites in territories.

Not only can vegetation conceal prey but prey may also select vegetation that allows them to watch predators (Embar *et al.* 2011, Camp *et al.* 2013). Enhanced vigilance might allow prey to utilise anti-predator strategies and avoid detection or capture (Samia *et al.* 2013). Prey can also use vegetation structure to facilitate rapid escape from predators (Camacho 2014) or to provide a safety screen against attack (Wirsing *et al.* 2007). Although heterogeneous vegetation structure can provide greater concealment, more potential nest and feeding sites, and therefore more potential prey sites, such heterogeneity also

leads to a spatially variable landscape of predation risk, or ‘fearscape’, that can also influence habitat and nest site selection by prey (Laundré *et al.* 2001, Arias-del Razo *et al.* 2012, Olsoy *et al.* 2015). If predation is important in habitat selection in nightjars we predict that nightjars will not nest in the densest vegetation within their song territories but will locate nests in vegetation of intermediate density to allow them to watch for predators.

Whereas some predation events are opportunistic (Schmidt 2004), learning, e.g., observing parental activity has been demonstrated in a number of predatory species including red squirrels (*Tamiasciurus hudsonicus*) (Pelech *et al.* 2010) and corvids (Sonerud and Fjeld 1987), and predators certainly use parental activity to locate nests (e.g., Bonnington *et al.* 2013, Haff *et al.* 2015). Parents can affect nest crypsis and this occurs in two ways; sit on the nest and conceal the eggs or defend the nest when predators are close and disclose its presence. Vegetative nest concealment and parental defence may react in complex ways, e.g., parents can compensate for poor concealment through incubation or defence but conversely reveal nests to visual predators (Cresswell 1997, Weidinger 2002). Predators might also use olfaction to detect nests but studies have produced conflicting results (e.g., Clark and Wodeser 1997, Ibanez-Alamo *et al.* 2014).

Clearly then, many factors determine nest site choice and habitat selection in birds (and this review is itself only a sample), and a consequence is that habitat selection may often be best understood on a population and species basis. I propose however that for ground nesting species like the nightjar, predation may be an overriding determinant of habitat choice. Nightjars nesting in commercial plantations might choose territories that are least affected by forestry operations or relocate nests after disturbance from deer. In particular, because nightjar eggs are not cryptic and background matched parental concealment might be important for reducing predation. If birds are forced to leave the eggs then vegetative cover might also be important in reducing predation.

The following study uses radio telemetry and territory mapping to determine the song territories of two populations of nightjars nesting in commercial lowland pine plantations and to measure vegetation characteristics and territory size and shape. At this point in the thesis I was not testing any specific theory on habitat selection in nightjars. The findings from this study are to be used in the following chapter to examine the relationship between habitat choice and nest predation in the context of nest disturbance. More specifically, the aims of this study are:

- i. to determine the nest site location of nightjars breeding in the two forests
- ii. to measure song territory variables of mated and unmated males including;
 - 1. size (ha)
 - 2. compactness ratio (see 3.2.5)
 - 3. proximity of nest to habitat boundary
 - 4. type of habitat boundary - hard or soft
 - 5. number of alternative nest sites
 - 6. vegetation characteristics at nest site - vegetation density, height and composition
 - 7. habitat selectivity

3.2 METHOD

3.2.1 Habitat categorisation

Using the spatial data analysis software package MapInfo Professional, stock maps (Sherwood and Lincolnshire Forest Enterprise 1994 and FC Dorset 1998) of the forests were digitised. The data supporting these maps is no longer available to the author. However, Sherwood has been digitised from the paper map that was originally used to do the habitat analysis in Mapinfo and redrawn using ArcMap version 10.2 to show how habitat was distributed (Figure 3.0). Unfortunately, there is no paper map for Wareham Forest but because the forests are of a similar age habitat categories were similar both in their composition and geometry. The major difference at Wareham was the more extensive and contiguous tracts of open heath. Each habitat type was recorded as a discrete polygon based on the following broad habitat types; clearfell (unplanted), divided

into grass clearfell (dominated by wavy-hair grass, (*Deschampsia flexuosa*) in Sherwood Pines and (*Molinia caerulea*) in Wareham Forest) and bracken clearfell (dominated by Pteridium), heathland (included both extensive blocks of common heather (*Calluna vulgaris*), bell heather (*Erica cinerea*), and cross-leaved heather (*Erica tetralix*) and fragmented patches along forest glades and rides). Conifer plantations were devolved by age and species with <4 year plantation containing conifer saplings of different species but predominantly Corsican pine (*Pinus nigra*), Scots pine (*Pinus sylvestris*) and Douglas Fir (*Pseudotsuga menziesii*), 4-9 year plantations with similar species composition to <4 year plantations, and finally 10-19, 20-29, 30-39, 40-49 and 50 years and over age categories. These age categories represent cycles of tree growth that have been shown to be important for nightjars nesting in other pine plantations in the UK (Bowden and Green 1991). Deciduous trees were classed by the majority species (tree planting data unavailable). In the majority of cases the land classification provided on the stock map allowed unambiguous identification of land use type, i.e. clearfell, tree age and type of tree species, heathland, agricultural, railway, track or road, and so on. When classification was unclear, visits to the area were made in order to determine, where possible, an appropriate class. However, a small number of polygons contained a mixture of tree species, e.g., birch and sweet chestnut, or conifers of different ages and were thus classified as 'mixed age'. Polygons with no planting year were classed as unknown. The datasets were converted from Microsoft Excel to a MapInfo table.

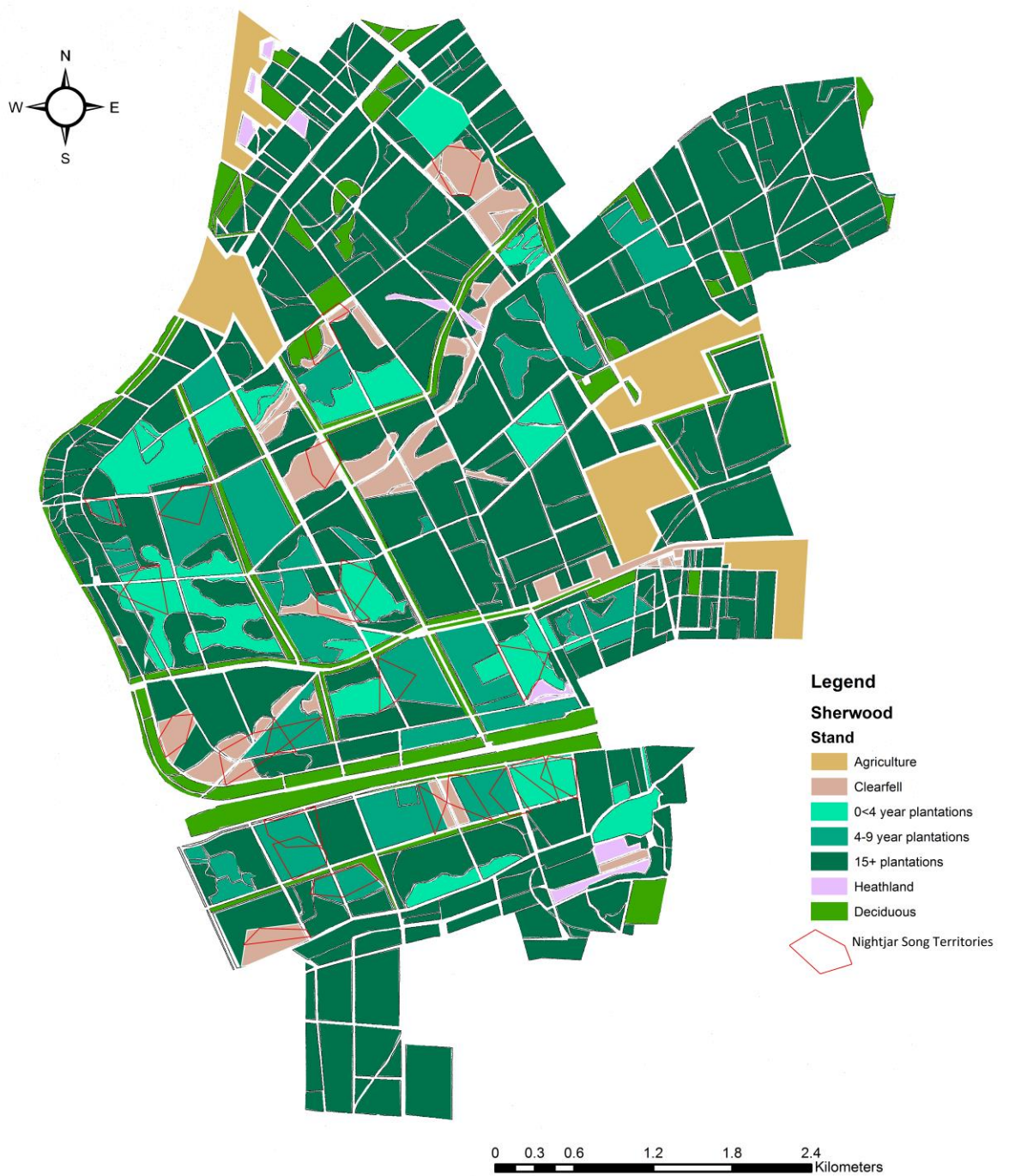


Figure 3.1 Digitised basemap of Sherwood Pines Forest Park showing major land use categories and nightjar territories.

3.2.2 Radio tracking

See the general methods section in Chapter 2 for details of the procedures for trapping and attaching radio tags and for radio tracking. If the nest site of an instrumented male was located no attempt was made to capture the female for the purpose of tag attachment. If her mate was untagged no attempt was made to tag him.

3.2.3 Population census and breeding status

Nightjars sing from song posts on or near the edge of their territory. Choice of song posts varies from branches high up (20m) on the edge of mature trees, to cross bars on pylons, and even from very low elevations (1 metre) or from the ground (bare substrate). Although territory boundaries may fluctuate during the breeding season, it is possible to obtain reasonably accurate measures of territory structure from multiple visits to the site (Cadbury 1981). One common approach for censusing nightjars is territory mapping which relies on mapping the locations of singing males. A number of studies have used territory mapping to describe the habitat characteristics of nightjar breeding territory with varied success (Berry 1979, Ravencroft 1989, Conway *et al.* 2007, Jiguet and Williamson 2010). However, potential limitation of this approach are territory overlap (sharing of song posts) leading to underestimates of populations, and counting of unmated males leading to overestimates (Bibby 2000, Sharps 2013). Factors that might further impact the precision of a census by causing territory boundaries to change include the late arrival of males to the breeding area, the passage of non-territorial males who may stop on migration and sing for one or two evenings, the failure or abandonment of nests (including those on adjacent territories) and mortality of adult birds. Finally, the establishment of second broods usually shifts the focus of activity to another part of the same territory, resulting in a boundary change and reformation of the territory. Steinke (1981) recorded changes in territory size between 1st and 2nd broods of c3.5 ha and c3.1 ha to c4.8 ha and c4.7 ha respectively (Cramp 1985).

To achieve an accurate census and determine territory characteristics, this study relied in part on the radio tracking technology and in part on detailed territory mapping (including data from previous years provided by ringing groups with extensive experience of working with nightjars (Birklands Ringing Group and Stour Ringing Group) and intensive fieldwork (including the help of volunteers) during the current arrival and courtship periods.

The radio telemetry would allow the identification of instances of territory overlap and the ability to distinguish between breeding and nonbreeding, as well as instrumented and noninstrumented birds giving greater precision to a population census. Knowledge of the behaviour of breeders and non-breeders including the strength and timings of their songs, and territory defence, coupled with familiarity with the fieldwork areas and the typically low number of singing nightjars would hopefully allow for an accurate census. Using behaviour to assign breeding status of male birds is commonplace (e.g., Guillemain *et al.* 2003) and the criteria for doing so in this study are outlined in Chapter 2, 2.2.1 'Capture techniques for adult nightjars'. However, changes in breeding status throughout the breeding cycle were anticipated so detailed field notes were maintained in order to detect any change in behaviour.

3.2.4 Song territory analysis

In this study 'song territory' and 'breeding territory' are used to describe the area of a bird's home range that is used primarily for breeding which includes courtship, copulation, incubation and brooding but not primarily for foraging and therefore belongs to category 'b' of Hinde's (1956) classification. Although birds also fed within their song territories foraging flights were recognisable as birds often flew directly to feeding patches normally outside their song territory and fixes on such birds were not included in the analysis of song territories. In order to account for outliers created by foraging excursions 95% minimum convex polygons (MCPs) based on churring positions were created for nightjar territories (n=52, Nottingham 26 and Dorset 26) as a data layer using Mapinfo Professional on the digitised basemap of the forests. The digitised versions of these maps are no longer

available. I have recreated territories at Sherwood Pines Forest Park using ArcMap version 10.2 for visual analysis only (Figure 3.1) Excursions occurred when birds left their breeding territory to forage or engage with conspecifics. These were clearly discernible from flights within the territory or between song posts. This was done by generating 'recalculated arithmetic mean peeled polygons' for each song territory (Kenward 1987). In very simple terms this involved the recalculation of the arithmetic mean centre of the remaining coordinates each time an outlier (i.e. coordinate farthest from the arithmetical mean of all locations) was removed. The major limitations of this approach are that fixes are considered individually, areas of high utilisation have same value as areas of low utilisation, territory estimation is sensitive to the number of fixes and is also likely to include 'unused' habitat (White and Garrott 1990). However, because MCPs replicate the method of territory mapping that is used in national bird surveys of song territory they are repeatable. For reasons highlighted above, song territories can change - e.g., breeding status of territory holder can change, so MCPs represent the territory held by each male for a known period of time (6 weeks) which allows for the rearing of a first brood. Territory boundary changes, due to second broods for example, were therefore not considered in detail in this study. The area of each habitat type (ha) within each song territory, similar to those used in the analysis of availability, were calculated in Mapinfo Professional as discrete polygons and converted to percentages. Only the area contained within the 95% MCP, based upon the song posts, was used in the analysis because the nest site was located within this area in all the sampled territories. Habitat visited during foraging excursions (nightjar home ranges) is not considered. Although the number of elevated song posts per territory was not measured territorial males also sang from low perches on brash (cut or fallen branches) and from the ground. Therefore I make the assumption that number of elevated song posts does not affect territory size.

Findings from this analysis were used to recreate nightjar song territories by 'drawing' artificial ones in suitable (but unoccupied) habitat on the basemap. This will be discussed in detail below. In short suitable habitat was measured in the same way as habitat

occupied by nightjars and statistical analysis showed no difference for all of the geometrical and vegetation variables.

3.2.5 Size and Compactness of Territories

The territory size and compactness-ratio, (*C-ratio*) i.e. the ratio of a polygon's area to its perimeter, of nightjar territories were measured using MapInfo Professional. The formula for the compactness-ratio is:

$$C = \sqrt{\frac{Ap}{Ac}}$$

Where *C* = the compactness ratio (*C-ratio*)

Ap is the area of the territory

Ac is the area of a circle having the same perimeter as the polygon under consideration

Ac is derived using r^2 .

A value of 1.0 indicates perfect compactness - a circle. The lower the value the greater the ratio of edge to area.

The importance of measuring the compactness ratio of nightjar territories can be viewed from the perspective of predator pressure. Assuming substrate and habitat homogeneity, a compact territory should theoretically be less susceptible to predation, due to the proximity of its perimeter to the 'centre'. According to Forman (1995), predators locate their foraging in edge environments because they support greater species diversity than interiors. Thus, in an elongated territory the ratio of the perimeter to the area is greater. Therefore, the edge is proximately closer to the 'centre' and so individuals in the 'centre' are more vulnerable to predation (Forman 1995). Therefore, instead of measuring the area of suitable nesting habitat compactness ratio takes into account where a male 'chooses' to locate his territorial boundary by accounting for how patchy or fine grained habitat structure is. Although predators will not detect a territory boundary unless it coincides with an actual habitat boundary nightjars do avoid nesting adjacent to hard edges so compactness becomes a measure of how territory holders perceive the predation risk. Furthermore, the incidences of territory overlap suggest that proximity of other males might not reduce territory compactness.

3.2.6 Distance of nest site from habitat edge

The distance of each nightjar nest was measured to the nearest habitat edge (defined as a change in vegetation height or type including tracks, water etc.). Edges were defined as 'soft', gradual transition in vegetative height and species (ecotone) across a wide band or 'hard', abrupt change in vegetation height and species across a short band. Linearity was not used to define edge type (Forman 1995).

3.2.7 Vegetation characteristics of territories

Small scale measurements were then made within the territories. These included microhabitat measurements of vegetation heterogeneity, i.e. density (when viewed from above or the sides), height, and species composition, and finally non-vegetative categories including number of alternative nest sites. Amount of fine vegetation characteristics such as moss and lichen were autocorrelated with number of alternative nest sites and were not included in analyses.

Foliage density was measured by placing a black and white chequered cube measuring 33.3 cm^3 in the nest patch and viewing it firstly from above, and then obliquely from 4 sides at a height and distance of 2m and counting the number of visible whole squares. The number of squares visible from above the nest was calculated as percentage visibility (see Major and Kendal 1996). Percentage visibility from the sides was calculated by adding the number of whole visible squares for each side (Major and Kendal 1996).

The height of the vegetation was determined by marking out four, 1m wide by 3m long transects, at 0° , 90° , 180° and 270° from each nest site. At 0.5m intervals along each transect the height of the tallest plant was recorded and a mean generated.

The number of alternative nest sites (locations deemed suitable by the researcher based upon nests in that habitat characterised by small areas of bare ground) were counted in a circular 3 m wide transect around the nest site but located 10 m from the nest site.

Amount of bare ground was not estimated because it was so widespread in many territories and especially those on clearfells.

3.2.8 Determining habitat selectivity. Randomly chosen nests and territories

This study is concerned with nest site specificity and territory attributes that might enhance fitness through predator avoidance, not general habitat selectivity. To test the importance of nest site selection and territory attributes a series of random nests and territories were created in patches already occupied by nightjars. This controlled for both habitat patch size and territory size. This negated the need for a detailed compositional analysis, such as Aebischer *et al.* (1993), i.e. measuring the proportion of habitats within territory versus proportion available in the study area (Johnson's (1980) second order selection). Nest site preference was determined by creating 100 randomly stratified nest patches and territories (20 in each of the different nesting habitats selected by nightjars) and comparing vegetation and other attributes to nightjar nests/territories in the corresponding habitat. The territory boundary was constructed by overlaying a polygon of the mean territory area and compactness ratio for that particular habitat type where nightjars were nesting. The nest site was chosen by placing a grid consisting of 2m² squares over the polygon and randomly selecting x and y coordinates from a random number table for each square in the grid to determine the location of each nest (Martin 1998). Where random numbers located a nest in habitat not included in that habitat category, or on tracks, buildings or other non-typical nest sites, a new set of coordinates was used. The territory variables 'area' and 'compactness ratio' were not measured for comparison with real nightjar territories but all the other variables were, as detailed above.

Statistical tests

Statistical tests included Independent t-test, ANOVA and where necessary Tukey post hoc tests. All analyses were done in SPSS version 21.

3.3 RESULTS

3.3.1 General habitat categorisation

The dominant tree species within Sherwood Pines Forest Park is Corsican pine, *Pinus nigra* var. *maritima*, with Scots pine *Pinus sylvestris*, mixed Corsican/Scots pine and Mixed Scots/Corsican pine (Table 3.1). Birch, *Betulaceae* is the most abundant deciduous species while chase, i.e. all the unplanted edge and ride habitats made up a further 259.89 ha. Heathland made up just 3.8 ha. Clearfell constituted 29.67 ha.

Previous forest design plans in the early 1990's at Wareham began the process of age class diversification and this is reflected in the fairly even distribution of woodland but with some large blocks of mature pines. The dominant land use category is coniferous woodland (1165 ha) consisting of Corsican pine and Scots Pine, mixed Corsican/Scots pine, Bishop's Pine, Maritime Pine, with Norway spruce and Douglas fir making up the majority of the remainder, with small pockets of Monterey Pine and Sitka Spruce. Broadleaved woodlands only constitute 40 ha and this was dominated by Beech and Birch. Open habitat including unplanted rides and heathland represents 338.3 ha (both wet and dry heath - 149 ha within Morden Bog) and unplanted clearfell 51.4 ha. The notable differences in the two locations are the absence of extensive deciduous firebreaks at Wareham Forest and the very small area of heathland at Sherwood Pines Forest Park (3.8 ha) compared to Wareham Forest (c249 ha) (Table 3.1).

The dominant land cover categories are summarised in table 3.1. All other land cover categories covered less than 5 ha and are not included individually. These include experimental plantings of eucalyptus, varieties of 'Christmas' trees, campsite and caravan-park, buildings, open water, unknown, etc. Collectively these constituted 19.24 ha (<1%) at Sherwood Forest and 41.2 ha (<3%) at Wareham Forest.

At both sites the main vegetative understory included wavy-hair grass (*Deschampsia flexuosa*), purple moor grass (*Molinia caerulea*), bristle bent grass (*Agrostis artisii*), mat-

grass (*Nardus stricta*), bracken (*Pteridium aquilinum*), fox glove (*Digitalis purpurea*), heather (*Calluna vulgaris*, *Erica cinerea* and *E. tetralix*) western gorse, (*Ulex gallii*) european gorse (*U. europaeus*) bramble, (*Rubus fruticosus*) birch (*Betula pendula*), pill sedge (*Carex pilulifera*), mosses such as (*Sphagnum papillosum* and *S. pulchrum* (Dorset), *Narthecium ossifragum*) and crimson fungus (*Hygrocybe mineata*) and lichens (*Cladonia floerkiana* and *Imadophila ericetorum*). Non vegetative categories include bare ground, tree stumps, ‘brashings’ (tree cuttings) and tracks.

Sherwood Pines Forest Park			Wareham Forest	
Land cover category	Area (Ha)	Percentage	Area (Ha)	Percentage
Corsican Pine	689.5	47.8	751.2	42.2
Scots Pine	53.6	3.76	85.8	4.82
Corsican Pine & Scots Pine	138.9	9.75	92.5	5.2
Bishop’s Pine	na	na	76	4.27
Mixed pine & deciduous	39.7	2.79	43.4	2.44
Maritime Pine	na	na	54	3.03
Norway Spruce	na	na	41	2.30
Mixed deciduous	47.7	3.74	40.9	2.30
Clearfell	29.7	1.98	51.4	2.89
Birch	20.6	1.44	18.2	1.02
Beech	8.5	0.59	6.7	0.38
Oak	7.4	0.52	7.9	0.44
Other deciduous	10.6	0.74	8.3	0.47
Chase (Inc. heathland)	259.9	18.25	338.3	19
Agricultural	73.7	5.17	61.5	3.45
Railway	33.9	2.38	na	Na
Other (e.g., open water)	19.2	0.99	41.2	2.31
Total	1423.7	100	1780.3	100

Table 3.1. Composition of generalised land cover categories within forests (immediate surrounds)

The dominant habitats outside the forest boundaries were cultivated arable land including watercress beds (Dorset) and colliery workings (Nottingham). Other land cover categories, as defined by the Nature Conservancy Council (NCC) (1993) are mineral works, colliery spoil heaps and tips (Nottingham), roads, urban, bracken and heather, new improved grassland, rough grass including marshland, open water (2.5 ha Old Decoy Pond, Morden

Bog, Dorset) allotments, camping, permanent pasture and meadow, and finally permanent pasture with mature trees and associated hedgerows.

3.3.2 Population census and breeding status

23 adult male and 7 adult female nightjars were radio-tagged (24 with tailed-mounted radio tags and 6 with backpack mounted radio tags). The birds were tracked using a hand held Marinar 57 receiver in order to determine their territories, breeding status and nest site locations. Using radio telemetry and territory mapping 23 territories (tagged males) and 29 territories (untagged males) were measured. From these (and the tagged females) 38 nests were located (Nottingham, n=21 (12 of which were radio tagged), Dorset, n=17 (9 of which were radio tagged). The nests were not marked in the field to avoid attracting predators (Haskell 1996). Instead, nest coordinates were taken using a Garam hand held Global Positioning System. The 38 nests were monitored from mid-May to mid-August during 1994 and 1998 until all birds had hatched or until the nest failed due to predation or abandonment. Because nests were found at different stages of incubation, egg (daily) survival rate was analysed using the Mayfield method (Mayfield 1975), and the confidence limits were calculated according to Johnson (1979). The breeding status of three tagged birds (2 Notts, 1 Dorset) could not be assessed. One of the birds shed the central retrice housing the tag, 4 days after instrumentation. The second bird left the forest, after losing the tag, and was re-trapped at the end of the breeding season, almost 6 miles further south. Similarly, an instrumented male left Wareham forest but the signal from the transmitter was located, using a light aircraft, approximately 2 miles north of the forest. The recovered tags were fitted to two other adult males. 3 birds (all males) changed their status from mated to unmated. In summary, territory data was collected for 52 birds (38 mated, 14 unmated), and nest site data on 38 birds. Of the 30 tagged birds, 23 male and 7 female, 14 males (61%) and 7 females (100%) were mated.

Of the 52 territories (38 mated and 14 unmated) it was estimated that at least 37 (71%) overlapped with a neighbouring territory. When the analysis was based on tagged males

only (n=21), 16 (76%) overlapped. In one instance territory overlap for 2 territories was estimated at 80% and 47% respectively. In the majority of incidents of territory overlap the percentage of the song territory that overlapped was <25% (range 2% to 80%). Birds typically made flights across territorial boundaries of neighbouring males but on occasion also shared churring posts or sang from within another's territory. A breeding male extended his territory to accommodate his second brood and encompassed the territory of a non-breeding male. The non-breeding male was recorded attending the chicks of the breeding male's first brood.

There were no significant differences in the mean song territory attributes for tagged and untagged birds so in the analysis of nest site choice and territories in the different habitat categories, both groups were pooled.

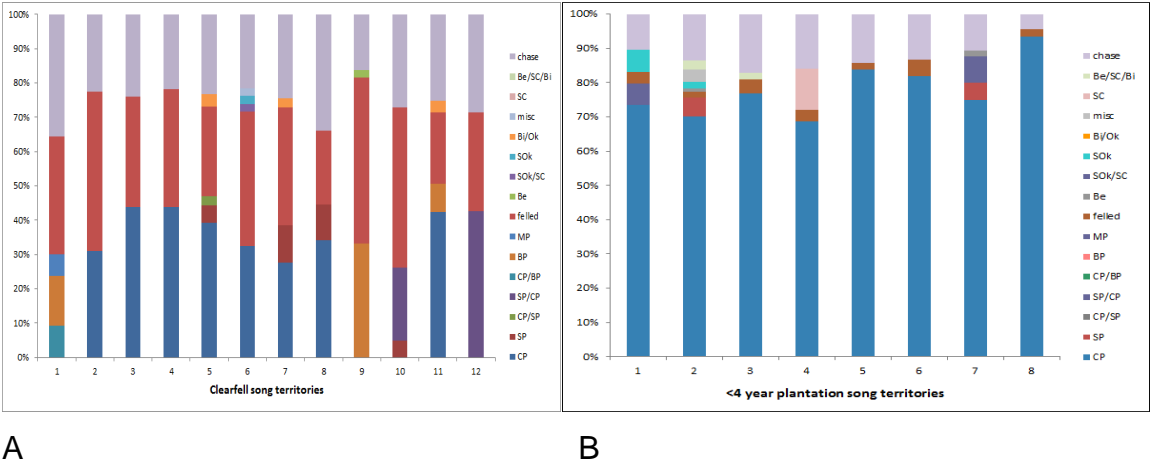
3.3.2.i Effects of breeding status on song territory size and compactness

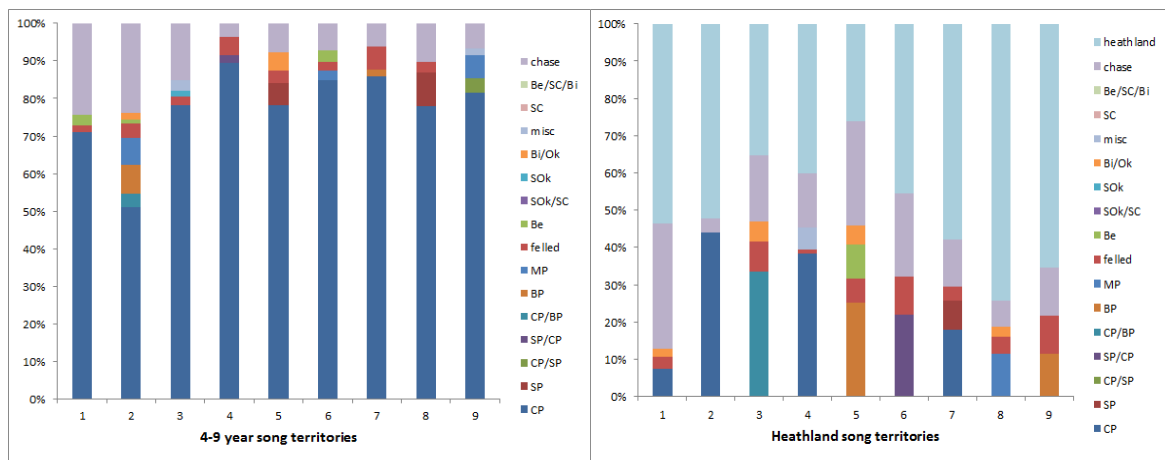
Although there was no correlation between breeding territory area and the number of churring fixes, (Pearson's, $r=.09$, $p=0.702$), a habitat level comparison between the mated and unmated males' territories was not undertaken because the number of unmated birds in each habitat category was too small and in some cases unmated males did not occur in a habitat category - e.g., heathland. However, data for mated and unmated males shows no difference for territory size (T-test, $t=0.83$, $df=1$, $p=0.41$), (mated mean 7.1 ha, range=3.25-18.98 ha, $se=0.4$, $n=38$; unmated mean 8.37 ha, range 3.3-23.8 ha, $se=0.82$, $n=14$) but territories were significantly less compact for unmated territory holders (T-test, $t=3.96$, $df=1$, $p<0.001$) (mated mean=0.66, range=0.39-0.91, $se=0.12$, $n=38$) (unmated mean=0.57, range=0.39-0.74, $se=0.03$, $n=14$). Two radio tagged birds were recorded singing at locations not included in their territory boundaries (830m and 1,080m from their territory boundary) but this was recorded once for each bird and might have coincided with a foraging excursion. All subsequent analyses are based upon mated males only.

3.3.3 Song territory analysis

3.3.3.i Vegetation composition

Prior to comparing the geometry of the territory (based on song posts and used mainly for breeding) of the 38 paired nightjars, a description of the plant species composition and age class of trees is provided along with other habitat categories. All 17 plantation song territories (Figures 3.2 B-C) were dominated by Corsican pine and it occurred in 8 out of 12 clearfell song territories (Figure A) and 4 out of 9 heathland territories (Figure 3.2 D). Figure 3.2, A-D. Scots pine, Bishop’s pine and Maritime pine, or mixed plantings made up the majority of the rest of the conifers. There were few deciduous trees in most territories. The latter are usually at the edge of the territories and may include churring posts. Chase was also present in all of the territories but this is unsurprising, as most compartments are surrounded by tracks or firebreaks which are fringed with narrow corridors of ecotone. Chase includes rides and glades and is characterised by fragments of heather and open vegetated verges dominated by grasses and bracken. The deciduous trees in the majority of territories were mature trees growing in firebreaks between the compartments of conifers and along chase. 4 other nests occurred in ‘other’ habitat including ‘experimental block’, containing c10m eucalyptus trees with heather understory, conifer plantations aged 12-15 years and 18 years and one on partially vegetated burnt ground that could not be reasonably categorised. These were not included in the analysis.





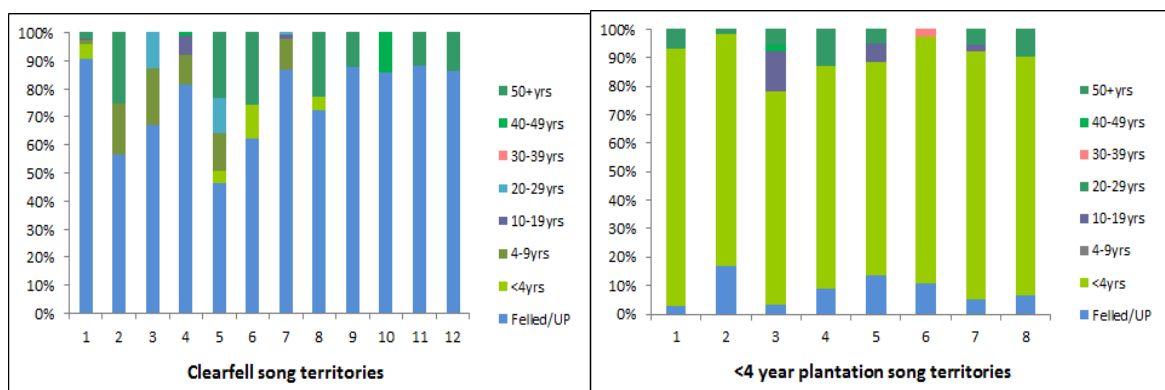
C

D

Figure 3.2. A-D. Vegetation composition of nightjar song territories in the different habitat categories, A - clearfell, including grass and bracken clearfells, B - <4 year plantations, C - 4-9 year plantations and D - heathland song territories. The abbreviations are as follows: Be – Beech: Bi - Birch: BP - Bishop's Pine: CP – Corsican Pine: MP - Maritime Pine: Misc. – miscellaneous: Ok – Oak: SC – Sweet Chestnut: SOk - Sessile Oak: SP – Scots Pine.

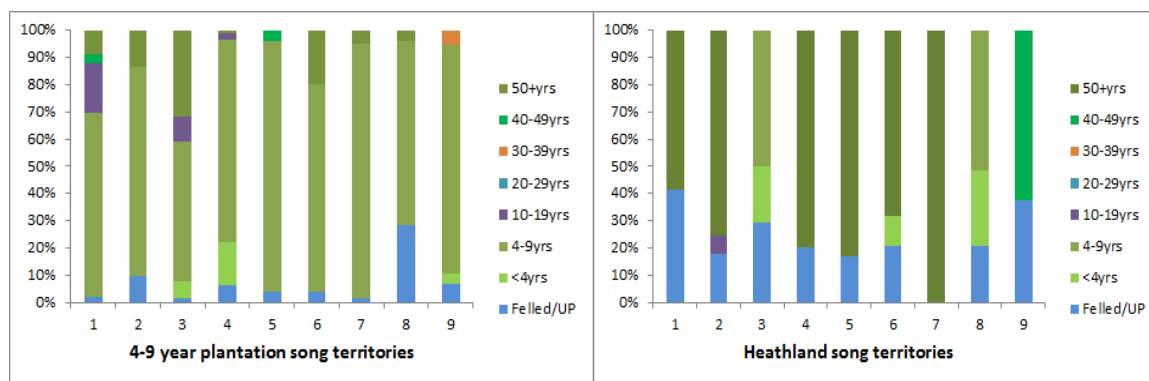
3.3.3.ii Age composition of coniferous trees in nightjar song territories

Despite the dominance of coniferous trees in the song territories, the age class is largely restricted to young trees, as shown in Figures 3.3 A-D, except for clearfell (Figure 3.3 A) and heathland (Figure 3.3 D). Eight of the territories were comprised primarily of trees younger than 4 years old (Figure 3.3 B). Trees aged between 4-9 years dominated 9 territories (Figure 3.3 C). In contrast, in territories on clearfell (7 out of 12) (Figure 3.3 A) and heathland (6 out of 8) (Figure 3.3 D) the dominant tree age category was 50+yrs. The category, clearfell occurs within all but one territory, and dominates twelve.



A

B



C

D

Figures 3.3 A-D. Age class of conifer trees within nightjar song territories based upon habitat type. A - clearfell, including grass and bracken clearfells, B - <4 year plantations, C - 4-9 year plantations and D - heathland song territories. Felled/UP - felled/unplanted.

3.3.3.iii Area

Nightjar territories were significantly different for mean area (ha) in different habitats (ANOVA, $F=16.07$, $df=4$, $n=38$, $p>0.001$ - Figure 3.4). Nightjar territories in 4-9 year plantations possessed a mean area of 4.56 ha ($se=0.23$, $n=9$) and were significantly smaller than grass clearfell (mean 7.51 ha, $p=0.006$, $se=0.59$, $n=6$), bracken clearfell (mean 9.03 ha, $p<0.001$, $se=0.86$, $n=6$) and <4 year plantations (mean 9.32 ha, $p<0.001$, $se=0.72$, $n=9$). Heathland territories possessed a mean area of 5.5 ha ($se=0.17$, $n=8$) and were significantly smaller than bracken clearfell ($p=0.001$) and <4 year plantations ($p<0.001$). Based upon the available habitat (Table 3.1) and number of nesting birds (male and female) sampled in this study the approximate breeding densities were as follows; grass clearfell, 0.36 birds/ha (33.6 ha), bracken clearfell, 0.63 birds/ha (19.1 ha), <4 year plantations 0.16 birds/ha (111.2 ha), 4-9 plantations 0.064 birds/ha (286 ha) and heathlands 0.062 birds/ha (254.8 ha).

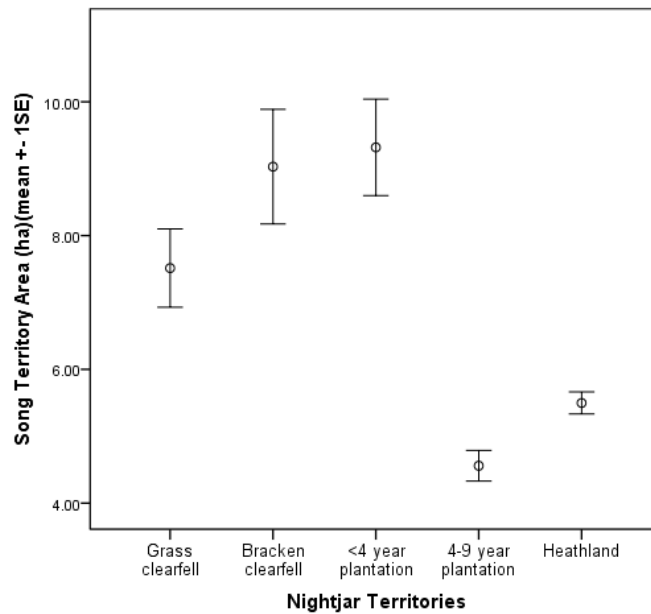


Figure 3.4 Comparison of song territory size for nightjars nesting in different habitats.

3.3.3.iv Compactness Ratio

Song territories in the different habitats possessed similar mean compactness ratios (ANOVA, $F=0.398$, $\text{mean}=0.66$, $\text{se}=0.012$, $\text{df}=4$, $n=38$, $p=0.808$), (grass clearfell, $\text{mean}=0.64$, $\text{se}=0.025$, $n=6$; bracken clearfell, $\text{mean}=0.66$, $\text{se}=0.027$, $n=6$; <4 year plantations, $\text{mean}=0.67$, $\text{se}=0.019$, $n=9$; 4-9 year plantations, $\text{mean}=0.68$, $\text{se}=0.034$, $n=9$ and heathland, $\text{mean}=0.65$, $\text{se}=0.12$, $n=9$).

3.3.4. Nest location analysis

3.3.4.i Distance to edge

Distance of nest to habitat edges in the different habitats was not significantly different; $\text{mean}=12.82\text{m}$, $\pm\text{SD } 7.52$ (ANOVA, $F=1.01$, $\text{se}=1.22$, $\text{df}=4$, $n=38$, $p=0.421$), (grass clearfell, $\text{mean}=14.3\text{m}$, $\text{se}=3.39$, $n=6$; bracken clearfell, $\text{mean}=15.2\text{m}$, $\text{se}=3.64$, $n=6$; <4 year plantations, $\text{mean}=9.56\text{m}$, $\text{se}=2.13$, $n=9$; 4-9 year plantations, $\text{mean}=11.1\text{m}$, $\text{se}=2.65$, $n=9$ and heathland, $\text{mean}=15.5\text{m}$, $\text{se}=2.28$, $n=9$).

3.3.4.ii Habitat edge

Nightjars were more likely to nest adjacent to soft edges (30 versus 8 nests) nesting a mean distance of 9.53m, \pm SD 5.9m, of similar vegetation structure in terms of height, and this was not affected by habitat type ($\chi^2=1.231$, $df=4$, $n=38$, $p=0.873$). However, they nested a mean distance of 17.38m, \pm SD 7.1m, from 'hard edges', characterised by much taller vegetation.

3.3.4.iii Nest site characteristics

There was a significant difference in the mean vegetation height and density surrounding nests in the different habitat categories (ANOVA, $F=106.8$, $df=4$, $p<0.001$ and $F=32.9$, $df=4$, $p<0.001$, $n=38$ - Figure 3.5 and 3.6) but not vegetation cover above nests ($F=2.18$, $df=4$, $p=0.093$, $n=38$) or number of alternative nest sites ($F=0.116$, $df=4$, $p=0.976$, $n=38$). Post hoc Tukey tests show that vegetation in grass clearfell was significantly shorter than bracken clearfell ($p=0.001$), and 4-9 year plantations ($p<0.001$), heathland vegetation was also shorter than bracken clearfell ($p<0.001$), and 4-9 year plantations ($p<0.001$), and <4 year plantations were significantly shorter than bracken clearfells ($p<0.001$) and 4-9 year plantations ($p<0.001$). Bracken clearfells had significantly shorter vegetation than 4-9 year plantations ($p<0.001$).

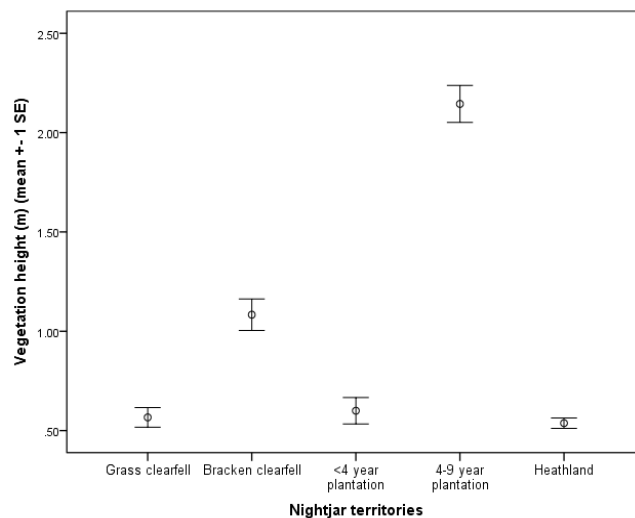


Figure 3.5 Comparison of vegetation height (m) (mean \pm 1SE) around nightjar nests in different habitats.

Vegetation density varied in a different pattern. Post hoc Tukey tests showed that nest sites on 4-9 year plantations were surrounded by significantly denser vegetation than nests on all other habitat categories; grass clearfell ($p<0.001$), bracken clearfell ($p<0.001$), <4 year plantations ($p<0.001$) and heathland ($p<0.001$) and nests on grass clearfell had significantly less dense vegetation than all other habitat categories; heathland ($p<0.001$), bracken clearfell ($p<0.001$), and <4 year plantations ($p=0.049$). Nests on heathland had marginal to significance greater vegetation density than <4 year plantations ($p=0.05$) (Figure 3.6).

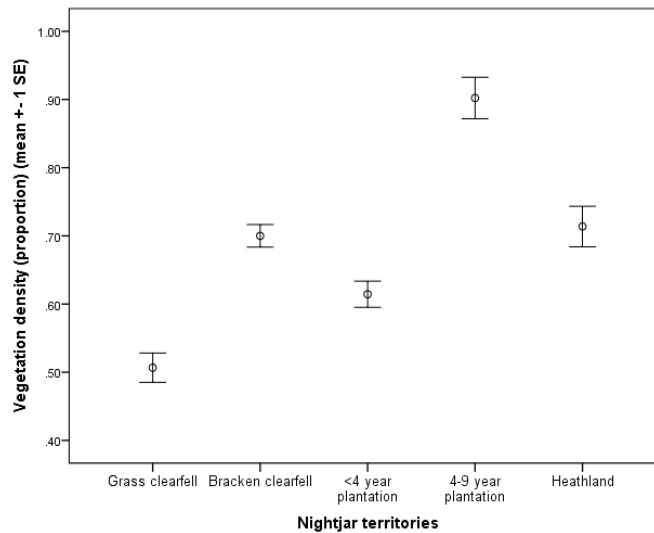


Figure 3.6 Comparison of vegetation density surround the nest (%) (mean ± 1 SE) of nightjar nests in different habitats.

3.3.5 Determining habitat selectivity: Random nest sites/territories

There was significant variation between nightjar nests and randomly stratified nests for all of the vegetation variables but this varied by habitat category (Table 3.2). In grass clearfell, <4 year plantations and heathland, there were significantly fewer alternative nest sites in randomly chosen territories than nightjar territories ($p=0.002$, $p=0.004$ and $p<0.001$ respectively - Figure 3.7). Vegetation height was significantly taller around nightjar nests in <4 year plantations but significantly shorter around heathland nest sites ($p=0.038$ and $p=0.005$ respectively - Figure 3.8). Vegetation cover above the nest was significantly lower at nightjar nests on bracken clearfells, <4 year plantations and 4-9 year

plantations ($p=0.014$, $p<0.001$ and $p<0.001$ - Figure 3.9). Vegetation cover around the side of nests was also significantly lower for nightjar nest sites in, bracken clearfell, <4 year plantation, 4-9 year plantations and heathland ($p<0.001$, $p<0.001$, $p=0.01$ and $p=0.013$) but not grass clearfell where it was higher ($p<0.001$) (Figure 3.10). The distance of the nest to a habitat edge varied significantly for nests in <4 year plantations wherein nightjar nests are closer to edges than randomly chosen nests ($p=0.047$) (Figure 3.11). Finally, nightjars were significantly more likely to nest adjacent to soft edges ($n=30$) versus hard edges ($n=8$) in comparison to randomly located nests (soft edges $n=43$, hard edges $n=57$), $\chi^2=14.281$, $df=1$, $p<0.001$).

Table 3.2. Independent samples t-tests for habitat variables for nightjar versus random nest sites in the 5 habitat categories. * denotes significant difference. In all cases df=1. Grass clearfell n=6, bracken clearfell n=6, <4 year plantation n=9, 4-9 plantations n=9, heathland n=8)

	Grass clearfell				Bracken clearfell				<4 year plantations				4-9 Plantations				Heathland			
	t	p	Mean diff	SE	t	p	Mean diff	SE	t	p	Mean diff	SE	t	p	Mean diff	SE	t	p	Mean diff	SE
Alternative nest sites	3.5	.002*	3.67	1.06	0.84	0.41	1.42	1.68	3.12	.004*	3.83	1.23	0.64	0.53	0.96	1.51	3.86	.001*	4.25	1.10
Vegetation height (m)	0.7	.047*	0.12	0.17	-1.00	0.33	-0.17	0.17	2.19	.038*	0.17	0.08	1.01	0.32	0.22	0.22	-2.09	.005*	-0.21	0.10
Vegetation cover from above	-1.3	.051	-0.08	0.06	-1.82	.014*	-0.22	0.12	-3.26	.001*	-0.44	0.13	-3.98	.001*	-0.38	0.10	-1.18	.08	-0.08	0.07
Vegetation cover from the sides	2.3	.001*	0.19	0.08	-2.70	.001*	-0.16	0.06	-0.72	0.48	-0.08	0.11	-2.79	.01*	-0.10	0.04	-2.68	.013*	-0.13	0.05
Distance to edge (m)	-1	0.31	-5.97	5.77	-0.83	0.42	-4.38	5.32	-1.44	.047*	-9.58	6.65	-1.66	0.11	-9.04	5.45	-1.54	0.14	-7.05	4.58

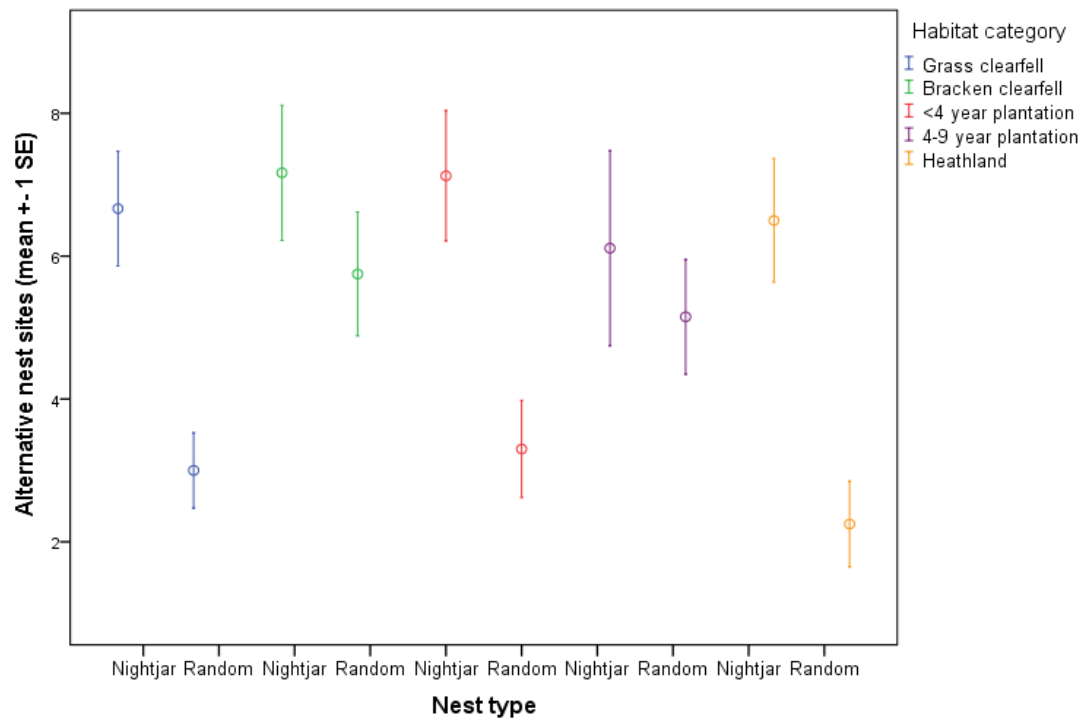


Figure 3.7. Comparison between number (mean \pm 1se) of alternative nest sites in nightjar territories compared to random territories.

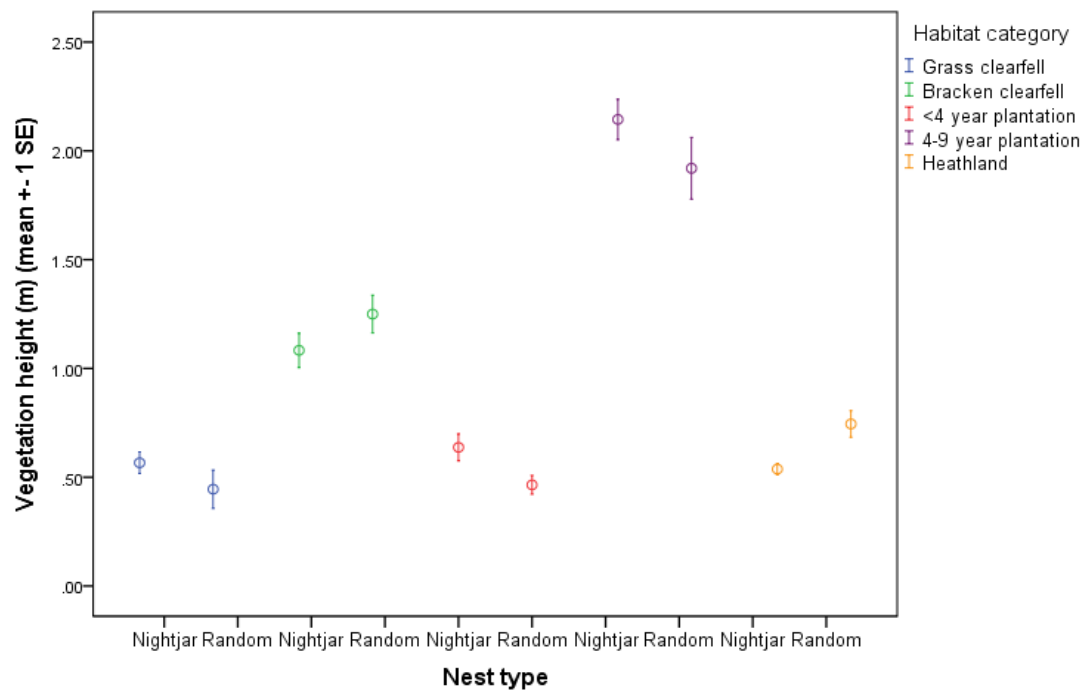


Figure 3.8. Comparison between the vegetation height (m)(mean \pm 1se) around nightjar nests compared to random nests

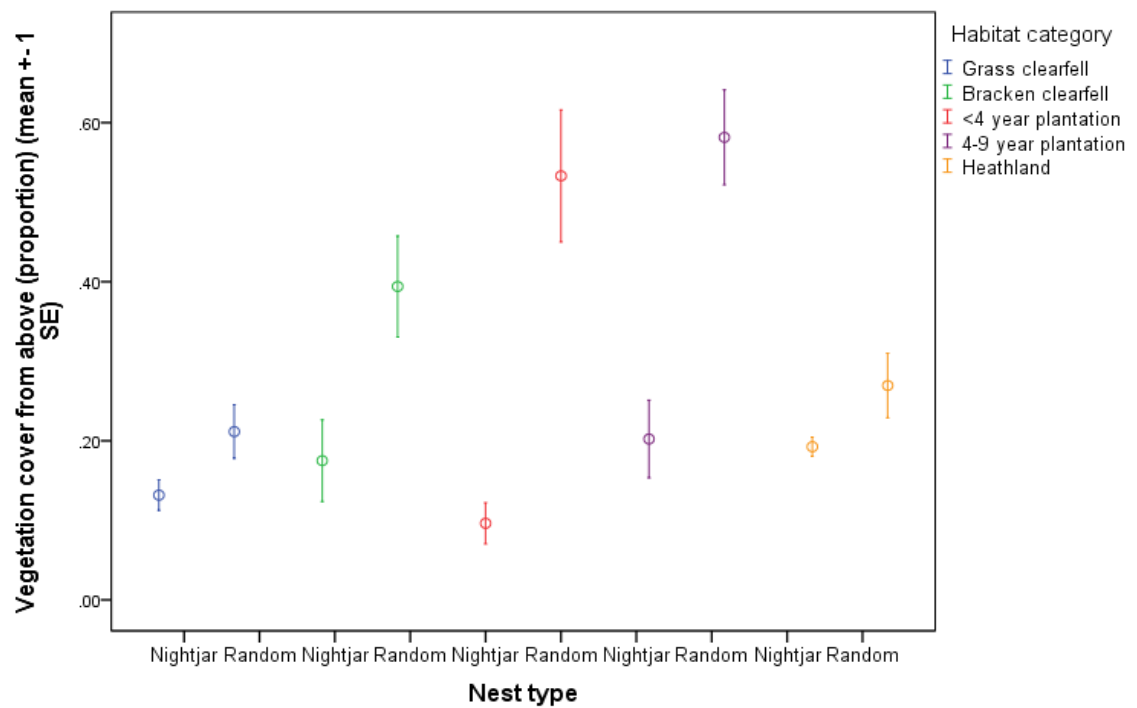


Figure 3.9. Comparison between the vegetation cover above (mean % \pm 1se) nightjar nests compared to random nests.

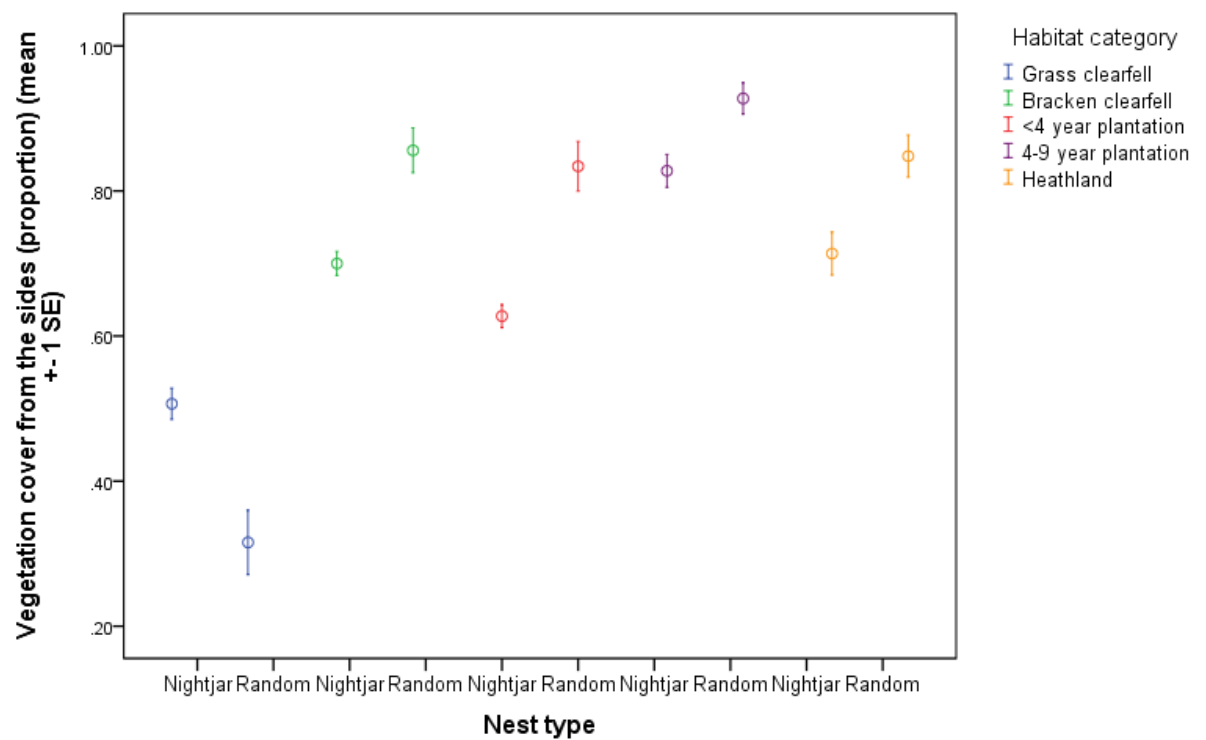


Figure 3.10. Comparison between the vegetation cover from the sides (mean % $\pm 1se$) at nightjar nests compared to random nests.

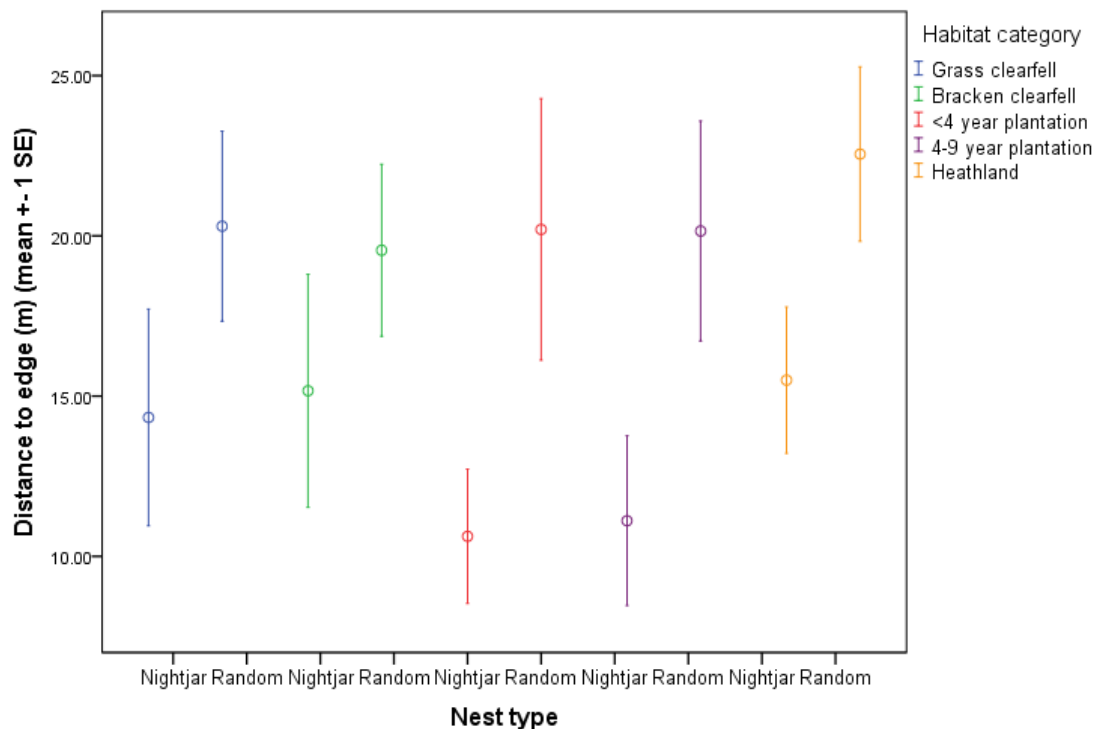


Figure 3.11. Comparison between the distances to a habitat boundary (m) (mean % $\pm 1se$) of nightjar nests compared to random nests.

3.4 DISCUSSION

Findings reveal that nightjars are conservative in their habitat choice and defend a breeding territory but do not defend foraging areas. In total territory attributes were collected for 52 male nightjars, and nest site data on 38 males (mated 73%). Of the 30 tagged birds, 23 male and 7 female, 14 males (61%) and 7 females (100%) were mated. Territory and nest site characteristics for tagged and untagged males were not significantly different so data were pooled for analysis. Territories of unmated males were significantly less compact than mated males but of a similar size. Territories and nests sites of mated males were significantly different for area, breeding density and vegetation height and cover surrounding the nest. Compared to random nests and territories there were significant differences for all the variables but this varied by habitat category. In

comparisons between nightjar and random nests both focal habitat patch and territory size were controlled for. These are discussed below.

A shortcoming of territory mapping is highlighted by the extent of territory overlap encountered in this study. Of the 52 territories it was estimated that at least 37 (71%) overlapped with a neighbouring territory and this rose to 76% when the analysis was based on tagged males only. In one instance territory overlap for 2 territories was estimated at 80% and 47% respectively (Figure 3.2). The extent of territory overlap should be considered when censusing nightjars and was also identified as a limitation of territory mapping in a more detailed study of nightjars by Sharps (2013) using Utilisation Distributions (Fieberg and Koehnann 2005) and the Bhattacharyya affinity index (Bhattacharyya 1943).

According to Donald (2007), if the Avian Sex Ratio (ASR) is skewed towards males, it is indicative that the population is under threat. Sex-biased dispersal is well-established for many species of bird (Greenwood 1980, Clarke, Sæther and Røskaft, 1997) and a meta-analysis by Dale (2001) found risk of extinction was higher in migratory species in small, isolated populations. This was due to female-biased dispersal, wherein, females have limited ability to locate mates when the population is fragmented and might disperse into unoccupied habitats. In this study, 73% of all the sampled males were mated. When the two study sites were compared 84% (21 out of 25) of males in the Nottinghamshire population was mated and 63% (17 out of 27) of the Dorset males. Despite the smaller size of the Nottinghamshire population, these data suggest that the Dorset population has a skewed ASR and might be under greater risk.

Nightjars show considerable natal and nest site philopatry however this is affected by gender and age. A SRG report (1994) shows that, 20 out of 38 males, and 11 out of 19 females, (ringed as adults in the previous year) returned to within 500m of their nest site. Adult females showed a tendency to be less philopatric moving further than males

between the first and second breeding season. For pulli and immature birds, the mean distance from the nest site (ringing site) to the retrap location was 6 km with 5 out of 22 birds recaptured within 500m of their natal site and there was an apparent westward movement. These data have important implications for the fate of this migratory species in the fragmented habitat mosaic that it is dependent upon. If females and immature birds are less philopatric territory holding males and prospecting birds may have a reduced chance of locating a mate (Weatherhead *et al.* 1994).

3.4.1 Broad vegetation composition of nightjar territories

In terms of the vegetation within territories, all of the 'planted' territories were dominated by Corsican pine and all territories contained chase (Figures 3.2 A-D). Nightjars discriminated for nesting in pine plantations younger than 10 years old, and expressed a preference for 4-9 year plantations and <4 year plantations (Figures 3.3 B-C). They also nested on clearfell and heathland (Figures 3.3 A and D). Eight of the territories were comprised primarily of trees younger than 4 years old and 9 contained trees 4-9 years (Figures 3.3 B-C). In contrast, in territories on clearfell (7 out of 12) (Figure 3.3 A) and heathland (6 out of 8) (Figures 3.3 D) the dominant tree age category was 50+ yrs. The category, clearfell occurred within all but one territory, and dominated twelve. The absence of mature trees in some territories shows that the territory holders did not regularly use them as churring posts but instead, used alternative singing-posts such as pylons, telegraph poles, and low perches. Such apparent selection for young plantations is demonstrated in the majority of studies including Ravencroft (1989), Alexander & Cresswell (1990), Bowden & Green (1994), Morris *et al.* (1994), Scott *et al.* (1998) and for nightjars nesting in Europe, Wichmann (2004) and Verstaten *et al.* (2011). However, the nightjars favoured plantations younger than five years in both Ravencroft's (1989) and Bowden & Green's (1991) studies, with the highest density of singing males located in restocked plantations three to four, and one year old respectively. Other studies including Hughes (1980) showed that 36% of nightjars nesting in downland forestry plantations in Sussex occupied conifers, and 12% on clearfells. This and other studies give support to the

understanding that such selectivity is not simply a function of proportional availability, but is a real preference.

The study by Morris *et al.* (1994) showed increases in plantation nesting nightjars, while other typical nesting habitats including heathland, experienced a decline. Between the period of the Gribble study in 1981 and the Morris *et al.* study in 1992, there was a 12.6% increase in the number of nightjar sites containing conifer plantations, associated with an increase in clearfelling and restocking. Indeed, the 1992 survey showed that young conifer plantations accounted for 54% of habitat records during the survey. Evidence for the cause of this increase is provided by the nightjar population of the Suffolk Sandlings. During the 1981 survey when mature pines covered the area, only four males were recorded. By 1987, Ravenscroft recorded 41 singing males and a 23% increase of logging of mature pines. The gale of 1987 left only 10% of the mature pines standing and by 1992 the number of male nightjars occupying the restocked areas had risen to 104 (Morris *et al.* 1994). In the Sherwood region, the 1981 nightjar census showed that 51.85% of nightjar records were assigned to coniferous habitat, whereas in 1992 this figure was 76.92%. Both figures support the observation that coniferous plantation was the only habitat category that was used in greater proportion to its availability. More recent surveys show sensitively managed pine plantations with inbuilt heathland restoration initiatives have become critical nesting sites for nightjars (Conway *et al.* 2007).

3.4.2 Alternative nest sites

It may be that habitats with numerous alternative nest sites provides more potential prey sites, i.e. more areas have to be searched by predators (Martin 1993). Comparison of nightjar nests to randomly selected nests showed that there were significantly more alternative nest sites surrounding nightjars nests on grass clearfell, <4 year plantations and heathlands (Figure 3.7). Finally, only one nightjar nest was predated by an adder in this study and this occurred on heathland. Alternative nest sites may be useful in the event of nest failure or they might reduce predation by increasing the number of prey

sites predators have to search (Martin 1993). This is supported by Burgess and Sorenson (1989), on heathland in Suffolk which showed that by increasing the number of small bare patches they increased their breeding nightjar population in subsequent years by providing nest sites and inadvertently reducing the likelihood of predation by increasing the number of basking sites for potential predators such as adders. Therefore possessing song territories with many alternative nest sites may enhance male fitness and be a good indicator of male fitness.

3.4.3 Nesting density

Birds nested at the highest densities on bracken and grass clearfell and lowest on 4-9 year plantations and heathland. Those on clearfells and plantations are surrounded by artificial boundaries, such as stands of mature pines, which delineate territories whereas those on heathlands, which is a more continuous and un-compartmentalised habitat have fewer such boundaries. The lower breeding density for 4-9 year plantations might be related to male age. Males nesting in 4-9 year plantations might have started nesting when the habitat was more open, are older, and when they die, new males are not recruited to the habitat. Because nightjars exhibit a degree of philopatry, most males return to breed in the same compartment during subsequent breeding seasons. Their familiarity with the habitat may give them a reproductive advantage over first-time breeding males, which may 'perceive' this habitat as unsuitable, or may be less able to compete for it (Schmidt and Whelan 2010, Piper 2011). A long term ringing study (BRG pers. comm 1995) of the nightjars nesting in the Sherwood Pines Forest Park has shown that birds occupying 4-9 year plantations are older and arrived later than birds nesting on the clearfells and recently planted compartments. Late arriving males may also use the presence of conspecifics as indicators of habitat 'safety' (Thomson *et al.* 2013) and arriving slightly later might allow them to make more optimal choices of territory and nest site (Loukola *et al.* 2012).

The breeding densities are higher than Liley and Clarke (2003) (0.01 birds/ha) and Conway *et al.* (2007) (0.008 males/ha) but comparable to a study on one of the same sites, Sherwood Pines Forest Park, 0.16-0.27 birds/ha (Lowe, Rogers and Durrant, 2014). However, these studies provided broad categories of 'available' habitat and Lowe *et al.* (2014) did not provide details about how they determined 'available' habitat and so direct comparisons cannot be made.

3.4.4 Song territory size

Nightjars nesting in 4-9 year plantations and heathland defended significantly smaller territories than conspecifics in other habitats (Figure 3.4) but all were of a similar compactness. Territory size varies between studies and can be as small as 1.5 ha and as large as 32 ha (Cleere 1998, Holyoak 2001). Berry (1979) recorded an average territory size for heathland nesting nightjars of 5-6 ha. Schlegal (1969) recorded territory sizes ranging from 3.8 ha to 6.7 ha. Unlike many species, nightjars do not defend foraging areas and therefore territory size is unlikely to be related to foraging requirements (e.g., Stenger 1958, Kesler 2012 but see Adams 2001 and Sharps, 2013). Foraging males at both study locations flew variable distances (Nottingham range ~30m to 1.020m: Dorset ~250 to >6000m) to feeding patches (of variable quality based upon light and sticky trap of flying invertebrate catches) but males defended the smallest territories adjacent to high quality feeding patches (based on light trap catches but data not presented here and supported by Sharps, 2013).

Other studies of habitat preference in birds have assumed that nesting density is positively correlated with habitat preference (Petit & Petit 1996, but see Pulliam 1988). However, territories were smaller for birds nesting on 4-9 year plantations and heathland. Males in both these habitats were more likely to have a contiguous territory boundary with a neighbouring male and for their territories to overlap. Therefore interactions between males might shape territory attributes through the balance of pressure exerted at boundaries (Adams 2001).

Territories on clearfell and <4 year plantations were larger and more isolated and therefore in the absence of territory boundary disputes no rules of movement apply. Furthermore, such habitat might be perceived as suitable by young incoming males attempting to acquire territories (Olsoy *et al.* 2015). Resident males might therefore defend large territories against prospectors to guard against extra pair copulations (Moller and Birkhead 1993) but it should be noted that females could engage in EPCs during foraging excursions. Finally, territory size might be related to an important density dependent factor in the life history of birds, predation (Ricklefs 1969). Nightjars might be able to defend 'small' territories in habitats that provide a balance between optimal amounts of cover to enhance crypsis but allow for maximum vigilance (Camp *et al.* 2013), and such cover is less widespread on clearfell and young plantations. Nightjars may therefore exert dominance over conspecifics by predation avoidance. Suitable nest sites might be the major limiting resource. Thus, birds nesting on clearfells and young plantations, may be displaying ideal despotic distribution, in that males in the more suitable habitat are preventing them from establishing territories there. Consequently, they are forced to occupy another habitat, although their payoff will be lower (Alatalo *et al.* 1985). Because areas of suitable habitat for nesting nightjars are isolated and fragmented, some individuals may be forced to occupy atypical and unsuitable habitat whereas more experienced individuals may be more likely to exhibit greater bias for good territories/nests sites (Schmidt *et al.* 2015).

Finally, the relationship between territory size and proximity to foraging habitat and prey abundance has not been discussed but unpublished results on flight distances of foraging adults and moth and sticky trap sampling within foraging habitat, suggest that territories are smaller when flight distances to foraging patches are shorter, and prey abundance within patches is higher. Sharps' (2013) results from radio telemetry and moth and beetle trapping suggest that home range size decreased as proportion of suitable foraging

habitat with 500m radius of the home range increases, but concluded that further work was required

3.4.5 Compactness ratio of song territories

No study has measured the compactness ratio of nightjar song territories, and few have looked at this aspect of other avian territories (Adams 2001, Kesler 2012), and thus conclusions regarding its significance are speculative. There was no effect of habitat type on territory compactness. This suggests that regardless of nesting habitat, 'compact' territories in homogenous habitats enhance fitness. It may be advantageous to the territory holder to defend a compact, rather than an elongated area because the ratio of area to perimeter is smaller (Grant 1968, Smith 1974), and is thus less costly to defend (Eason 1992) against intruding males. Non-mated males defended significantly less compact territories suggesting that territory shape might be related to breeding status. A compact territory allows the male to locate his nest site away from the territory boundary, and thereby reduce the likelihood of predation or cuckoldry. Scott *et al.* (1998) found that the size and shape of the plantation significantly explained nightjar occupancy in that long narrow patches were avoided and this may be attributed to the need for plantations to accommodate more spherical territories. Wichmann (2004) found that nightjars would not establish territories on clearing less than 50 m wide.

3.4.6 Nest location in relation to habitat boundary and edge type

The distance at which nightjars located their nests from a habitat boundary and the nature of the boundary, hard or soft, did not differ significantly between habitats. However, there are certain conclusions that can be drawn. Nightjars nested closer to soft edge (mean=9.53m, \pm SD 5.9m) compared to hard edges (mean=17m, \pm SD 7.1m). However, comparison between nightjar and randomly chosen nest sites shows that nightjars nest closer to edges than would be expected by chance (Figure 3.11). Nightjars were also significantly less likely to nest adjacent to hard edges compared to randomly located nests suggesting that there is a selective pressure to avoid hard edges. It is likely that predation

pressure is greater along harsh habitat boundaries (e.g., Angelstam 1996, and Lahti 2001). The relationship between habitat edge and predation will be explored in the following chapter.

3.4.7 Vegetation characteristics in song territories

With regard to small-scale vegetation measurements within territories in the different habitats, there were significant differences in vegetation height (Figure 3.5) and cover around the nest (Figure 3.6) but not in cover above the nest or number of alternative nest sites. The differences can be explained by the age of the plantation. 4-9 year plantations contained taller pine trees with a mean height of 2.14 meters. The trees also had a greater girth, and number and density of branches. These factors, coupled with the presence of other plant species, including bracken, bramble and heather, created a higher density of foliage around nightjar nests than in any other habitat types. Heather species, including *Calluna vulgaris*, *Erica cinerea* and *E. tetralix* also grew better on the older plantations forming a natural understorey. Areas of bracken and grasses were favoured for nesting on the younger plantations and clearfells. Mean vegetation height on the <4 year plantations, grass clearfells and heathland were similar but the nests in heather had significantly greater vegetative cover surrounding them and were similar to nests in bracken clearfells. This has important implications for the effects of nest site disturbance because nightjars have been shown to ‘flush’ (fly from nest) earlier when surrounded by dense vegetation at sites with high levels of disturbance (Woodfield and Langston 2004). This will be discussed below.

3.4.8 Comparison between nightjar and random nests

Nightjars located their nests in a limited range of habitats and a second analysis revealed that they were also selective at a finer resolution. Analysis of nightjar nests and territories compared to random stratified nests and territories showed significant differences for most of the variables (Figures 3.7 - 3.11 - Table 3.2) suggesting that nightjars are selective in terms of vegetative cover within the range of habitats available to them. For example,

vegetative cover around nightjar nests was significantly less than at random nests in all habitats except grass clearfell (Figure 3.10). This supports the trade-off hypothesis by Gotmark (1995) who suggested that the song thrushes in their study were selecting nests sites with intermediate vegetative cover to allow them to see predators. Nests on grass clearfell, <4 year plantations and heathland had significantly less cover from above than randomly selected nests sites (Figure 3.9) suggesting that concealment from aerial predators might not be important in nest site choice. However, in all of the nests on the 4-9 year plantations, 6 out of 8 nests on <4 year plantations, 5 out 6 nests on bracken clearfells and 3 out 6 nests on grass clearfells there was an apparent escape route - a flight path where the vegetation was less dense and not overhanging the nest. All heathland nests lacked much overhanging vegetation although 8 were located within 2 meters of a tree (e.g., *Betula* spp.). Such ease of escape allows nightjars to sit very tightly and delay fleeing the nest and thereby avoid disclosing its presence. This requires good vigilance and a rapid escape (Camp 2013). This apparent selection is unlikely to be coincidental and demonstrates intrinsic factors (e.g., concealment for predator avoidance and vigilance) that govern habitat choice. Red-necked nightjar, (*Caprimulgus ruficollis*) also employ a vegetation shield and rapid escape route when foraging from roads at night (Camacho 2014).

Thus it can be argued that choice of nest site may be influenced by the selective advantage afforded by vegetative cover that provides sufficient concealment and an escape route, while allowing maximum vigilance, as birds located the majority of their nests in vegetation of intermediate density. Bowden & Green (1991) showed that nightjars nesting in pine plantations in Thetford, Norfolk preferred plantings of 3-5 years, and nested within vegetation with 'little height (<5 cm) or vertical structure' based upon acid soils. Regression analysis found a positive correlation between higher than average amounts of fine debris, moss, both short and long grass, bracken and shrubs, and nightjar occupancy but they concluded that there was 'no evidence of complex relationships between nightjar occupancy and cover variables, such as the existence of optimal

amounts of cover.’ (Bowden and Green pg 32, 1994). Scott *et al.* (1998) did find a relationship between amount of herbaceous cover and site occupancy concluding that ‘openness’ was a determinant of nest site choice. Nightjars are clearly selecting for cover but whether birds at Thetford are selecting intermediate cover from the range available is unknown and a recent study on the same population did not consider vegetative attributes of song territories (Sharps 2013).

Berry (1979) noted that nightjars avoided nesting in dense bracken in favour of small clearings amongst heather. Large continuous matrices of heather occur at Wareham Forest and provide what appears to be optimal nest cover. Despite the availability of small areas of heathland at Sherwood Pines, only one pair nested in it in 1994. In areas where conifers do not grow well, heather was allowed to grow as part of the Forest Enterprise’s heathland management strategy. These were located in frost hollows where ground temperatures allow cold moist air to develop and this is the main environmental factor that inhibits tree growth in these areas (pers. comm. Barwick). Consequently, ground frosts may occur later in the season than other areas in the forest, thus delaying, or even prohibiting, nest establishment by nightjars. Interestingly, numerous authors consider later than average ground frosts associated with protracted cold wet springs, as a cause of the decline of nightjars in the UK (Berry 1979; Berry & Bibby 1981; Cramp 1985).

Nightjars are clearly selective in terms of the habitat they choose to nest as randomly located nest sites within randomly stratified territories differed from real nests and territories with regard to all habitat and spatial variables. Nightjars have clearly benefitted from nesting in commercial pine plantations as a result of changes in forestry management (e.g., Open Habitats Initiative) and restoration of heathland within forests. However, despite the provision of suitable habitat sites remain unoccupied and it is likely that other limiting factors, such as prey availability, are operating (Langston 2007b). Another potential limiting factor might be disturbance (e.g., Liley and Clarke 2003, and this is the focus of the following chapter.

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CHAPTER FOUR

THE EFFECTS OF HABITAT SELECTION AND RESEARCHER ACTIVITY ON THE NESTING SUCCESS OF THE NIGHTJAR *CAPRIMULGUS EUROPAEUS*: A COMPARISON BETWEEN REAL AND ARTIFICIAL NESTS

Abstract

Predation of ground nesting birds is a significant cause of nest failure and this is exacerbated in degraded habitats. Therefore, predator avoidance is likely to be a key mechanism for habitat selection in birds, with individuals competing for the most optimal habitat. In birds with low nesting densities and which are difficult to study, artificial nests experiments can provide important insights into patterns of predation and provide useful information for conservationists and habitat managers. However, while studying a target species, researchers might inadvertently augment predation by disclosing nests or by providing artificial cues for nest predators. This study compared nest predation and daily nest survival (DSR) for nightjar and artificial nests (baited with quail and plasticine eggs) in 2 lowland nightjar populations nesting in commercial pine plantations in relation to habitat selection and degree of human visitation. Depredation on artificial nests was not significantly different to nightjar nests, suggesting that predators were responding to them in a similar way. However, predation of nightjar and artificial nests containing quail nests was mainly avian, whereas mammals accounted for the majority predation of artificial nests containing a plasticine egg. The key finding in relation to nightjar ecology is that habitat was the single best predictor of variation in depredation, along with edge type and whether the nest was visited or not. In terms of the different habitats (and nest types) depredation was significantly higher on nests in grass and bracken clearfells, followed by <4 year plantations and lowest in 4-9 year plantations and heathlands. Both nightjar and artificial nests adjacent to hard edges were significantly more likely to be depredated. The main effect of visit status on predation was caused by a higher nest success of visited artificial nests on bracken clearfells and <4 year plantations. Nests were depredated more rapidly in large territories and when adjacent to hard edges. In contrast, nest survival increased in tandem with increased vegetation density and territory compactness ratio. These results have important implications for habitat conservation initiatives for this species nesting in commercial pine plantations.

4.1 INTRODUCTION

Studies on ground nesting birds, especially those nesting in open habitats (e.g., Yanes and Suarez 1995 but see McKinnon, *et al.* 2010) have shown that nest predation, which is the most significant cause of nest failure (Moreau 1944; Skutch 1949; Martin 1992, 1993), increases in tandem with elevated levels of human visitation - both research activity and public activity (Bayne and Hobson 1997, Clark and Wobeser 1997, Hein and Hein 1996, Olson and Rohwer 1998, Mallord *et al.* 2007, but see Hammond and Forward 1956, Armstrong 1996, Sedinger 1990 and for a review, Ibáñez-Álamo, Sanllorente and Soler 2012). The breeding success of ground nesting birds can be reduced by human disturbance - e.g., recreational including off-road vehicles resulting in nest abandonment (Anderson and Keith 1980), increased predation of eggs and young due to reduced nest attendance (Giese 1996, Verhulst, Oosterbeek and Ens 2001), or the direct destruction of nests (e.g., waders and terns reviewed by Hockin *et al.* 1992).

Nests of nightjar, along with those of other ground nesting birds may be particularly vulnerable to predation, (Cramp 1955; Ricklefs 1969) especially if adults are disturbed during the day, leaving their eggs or chicks exposed to predation or desiccation (Ingels *et al.* 1982; Yanes and Suarez 1995; Lowe *et al.* 2014).

This study uses findings from the study in Chapter Three to measure the effects of habitat selection and researcher activity on nest predation rates and nest survival using a comparison between actual nightjar and artificial nests. It begins with a review of the key literature that has investigated the utility of artificial nest experiments as surrogates for predation of real nests, focussing then on literature that has considered the effects of researcher activity on nest survival.

4.1.1 Problems in comparisons of predation of real and artificial nests

Artificial nest experiments have helped formulate and test theories on nesting biology and

habitat selection in birds. Despite early warnings by Hammond and Forward (1956) about the inadequacy of artificial nests experiments as surrogates for experiments on real nests studies of this kind were increasing exponentially in the early 2000's (Moore and Robinson 2004), and despite the findings of important reviews (e.g., Major and Kendall, 1996) few are methodologically sophisticated enough for their findings to mimic those of real nests.

Such research has provided information on the relative significance of predator assemblages (Andren 1992, Bayne and Hobson 1998; Thompson and Burnhams, 2004; Røttereng and Simonsen, 2010), and vulnerability of specific nest types (Moller 1987, 1990; Burke *et al.* 2004; Purger *et al.* 2008; Djomo, *et al.* 2014). Studies have demonstrated different rates of predation between habitats with varying levels of concealment, (Gotmark *et al.* 1995, Burhans and Thompson 1998; Pehlak and Lohmus, 2008). Nest predation has also been studied at varying degrees of fragmentation, (ArangoVelez and Kattan 1997; Stephens *et al.* 2004; Githiru, Lens and Cresswell, 2005), habitat edge effects (Ries *et al.* 2004), including, distances from edges (Poysa *et al.* 1997; Svobodová, 2012; Vetter, 2013) and types of edge including ecotones, (Moller 1989), wetland-meadow - boundary (Suvorov, Svobodová and Albrecht, 2014), and roads (Bergin *et al.* 1997; Pescador and Peris, 2007). Finally, studies have emphasised the role of nesting density (Burke, *et al.* 1998; Gunnarsson and Elmberg, 2008) and helped to explain avian species assemblages, (MacArthur 1972; Martin 1988; Hromada 2002; Lima 2009) and resource partitioning (Martin 1998). However, due to methodological flaws, and assumptions that predators respond similarly to both natural and artificial nests, findings from some studies should be viewed with caution, especially given that they often present contradictory results (e.g., Robinson, Styrsky and Brawn, 2005). Faaborg's (2004) conclusion that the only way to measure predation is to study real nests (e.g., Flaspohler, Temple and Rosenfield, 2001) has merit but as Villard and Part (2004) suggest, a careful calibration between the focal species and indirect estimates of reproductive success provides important and useful information about difficult to study species.

4.1.2 Comparing predation rates and predators

Despite the problems that are associated with attempting to compare the predation of artificial nests with those of natural nests the justification for attempting to do so in this study is based on the majority evidence that predation of artificial nests is generally higher than that of real nests (MacIvor 1990; Berg 1996; Valkama *et al.* 1999; Berry and Lill 2003, Mezquida and Marone 2003, Lindell *et al.* 2004, Batáry and Báldi 2005, but see Davison and Bollinger 2000, Thompson and Burhans 2004). However, numerous studies have found conflicting results regarding predation rate of natural versus artificial nests (Moore and Robinson, 2004). Disparities in predation rates between real and artificial nests might be caused by researcher activity, choice of egg, choice of nest site and absence of parental activity at nest and these will be considered in more detail. For example, type of egg used in the nest experiment might also be important. Quail eggs experienced lower rates of predation than plasticine eggs because small mammals were unable to penetrate the shell, but could leave marks on plasticine eggs (Bayne and Hobson 1997). In contrast, a study by Ortega *et al.* (1998) revealed higher initial rates of depredation of natural nests containing quail eggs compared to artificial nests. However, a minority of studies including Davison and Bollinger (2000), showed predation of real nests of grassland birds to be higher (41% after 12 days of incubation), compared with artificial nests (13.5%).

Factors affecting predation are unlikely to work in isolation. For example different eggs to the target species, such as quail or plasticine might also attract different predators but this might not be because the eggs are different but that the absence of the parent at artificial nests determines depredation. For example, eggs of black grouse *Tetrao tetrix* nests were predated by mammals whereas those baited with chicken eggs were preyed upon predominantly by birds (Willebrand and Marcstrom 1988). They concluded that ground predators were following the scent left by the incubating female as she walked into the nest. However, because this behaviour is prevalent in many ground nesting birds, including nightjars, it is unlikely that it is maladaptive, but is likely to be less detrimental than flying directly into the nest (see also Storaas 1988). There are many potential reasons

why predation rates between real and artificial nest might not be equal and these are discussed in the following sections.

4.1.3 Predator identification and egg choice

Evidence from the above studies suggests that artificial and real nests are exploited by different predators. Furthermore, the identification of such predators has traditionally been a shortcoming of experiments using artificial nests. Methods of identification range from the visual identification of potential predators in the experimental area, to remotely triggered camera set-ups at nest sites (Bayne *et al.* 1997), and miniature video cameras, (Pietz and Granfors 2000; Thompson and Burhans 2004), and small time-lapse camera systems with infrared illumination for night time (Benson, Brown and Bednarz 2010). Greased boards covered with sand have also been used to identify the footprints of predators (Angelstam 1986), but this is unreliable (Huhta *et al.* 1996).

Plasticine eggs may be unreliable for identifying predators down to the species level because of overlap in tooth sizes in mammalian predators (Bayne *et al.* 1997), and in cases of predation of eggs by multiple predators (Lariviere and Messier 1997). Identification of predators of artificial wader nests is possible using plasticine eggs. Bill markings left in plasticine allowed researchers to distinguish between three species of corvidae (1989), and characteristics of mammalian and avian predation on wader eggs allowed researchers to identify mammalian predators from species specific tooth markings for hedgehog Erinaceinae and four species of mustelid (Green *et al.* 1987).

Another reason why plasticine eggs might not provide realistic estimates of predation is that they may provide olfactory cues for predators, and this has been shown to initiate predatory responses (Clark and Wobeser 1997; Rangen, Clarke and Hobson 2000). Disguising such cues by coating plasticine eggs in rubber solution reduced predation of artificial nests suggesting that olfactory predators were attracted to the novel odour of the plasticine (Purger *et al.* 2012).

Numerous authors have emphasised the inherent problems of using quail (*Coturnix japonica* and *Xexcalfactoris chinensis*) eggs for comparative studies (Lewis and Montevecchi 1999; Maier and DeGraaf, 2000). Eggs that are too large or too small in relation to those of the focal species will experience differential predation rates and attract different predators (Ettel *et al.* 1998, Svagelj, Mermoz, and Fernández 2003). Niehaus *et al.* (2003) found that quail eggs exaggerate edge effects through increased predation. Artificial eggs might not provide accurate estimates of predation in fragmented or mosaic habitats. For example, when nest survival was based on predation of quail eggs, the survival chances of ground nests in clearings is greater than at the forest edge or inside the forest but when based on plasticine eggs nest survival in clearings was lowest (Purger, Mészáros and Purger 2004).

Clutch size might also be an important determinant of predation risk. For example, artificial nests with varying numbers of eggs suffered different rates of predation and in particular that nests with fewer eggs are harder to find (Gotmark *et al.* 1995).

Both egg colouration and patterning have been shown to affect predation rates between nests (Yahner and DeLong 1992) and predatory responses (Stoddard, Marshall and Kilner 2011). In their review, Major and Kendal (1996) showed that only 14.5% of the studies using artificial nests used eggs that approximated to at least one of the target species in terms size, colour, number, and patterning. Visual predators may overlook asymmetric eggs (Lloyd *et al.* 2000) in a nest because their search image has evolved to detect symmetrical objects (eggs) which are of similar size, shape, colouration, and appropriate number, and use the symmetry as a stimulus to investigate. Predator search images might be calibrated to specific substrates and if eggs are placed on inappropriate ones they may be overlooked (Chase 2002).

4.1.4 Egg laying period

Another shortcoming of many studies using artificial nests is the period when they distribute their eggs. Nightjars generally lay their eggs in coincidence with the lunar phase (Cresswell 1992, Perrins and Crick 1996, Cleere 1998). If a full moon occurs during the arrival period of nightjars on their nesting grounds then egg-laying is synchronised to coincide with it. In some extreme examples, studies conducted their experiments outside the breeding season (e.g., Cresswell 1997) when predators' search images might have refocused on other prey (Sieving and Willson 1998, Langley *et al.* 1999, Stephens *et al.* 2007). Therefore, in order to mimic natural predation, one should set out the experimental nests in coincidence with the species under study.

4.1.5 Parental activity at nest

Predators may rely on parental activity to locate nests and according to the Skutch hypothesis nest predation increases with activity at nests (Skutch 1949). Activity of adult birds at a nest may be an important cue for predators, (Martin, Scott and Menge 2000, Bonnington *et al.* 2013 but see Roper and Goldstein 1997), or in the case of brood parasites in Yahner and DeLong's (1992) study. Berg (1996) found that predation rates were higher on artificial wader nests than natural ones, and postulated that active defence of adults at real nests reduced the opportunity for predation. He also suspected that selection for safe nest sites precluded birds from choosing those sites with higher risk of predation. Calls of nestling might act as a cue to predators and increase predation (Haff and Magrath 2011) but presence of parents to warn offspring should offset this (Haff and Magrath 2013) but this is affected by nest crypsis (Haff *et al.* 2015). The absence of defensive parental behaviour at artificial nests results in higher predation (Cresswell 1997, King *et al.* 1999). Effects can therefore be both positive - nest defence, Montgomerie and Weatherhead (1988), or negative - nest disclosure, Martin *et al.* (2000). Positive effects might outweigh negative ones because parents defend their nests by attacking and distracting predators, or by sitting on the nest and camouflaging it (Montgomerie and Weatherhead 1988; Weidinger 2002). The presence of an adult bird near the nest

discourages predators through active nest defence (Schmidt and Whelan 2005). Camouflaging artificial duck nests with 'dummy' birds prevented predation (Opermanis 2004), and artificial nests attended by a dummy red-backed shrike (*Lanius collurio*) were predated less than unattended nests and this was attributed to the aposematic colouration and aggressive behaviour of red-backed shrikes (Trnka, Prokop and Batáry 2008). Finally, predation of artificial nests in lapwing *Vanellus vanellus*, colonies was 26% that of the control group (nests without lapwing protection) (Goransson *et al.* 1975)

Artificial nests have also been used to measure rates of brood parasitism but might not provide accurate rate comparisons to wild birds due to the absence of parental activity at the nest. For example, rates of parasitism differed between real and artificial nests wherein 26% of active wood thrush nests (*Hylocichla mustelina*), and none of the artificial nests were parasitised by brown-headed cowbirds (*Molothrus predators*). They suggested that predators and parasites used parents to guide them to the nest (Wilson *et al.* 1998).

4.1.6 Density effects

Other problems associated with making comparisons between depredation of natural and artificial nests include density effects. Rarely do studies target only one species (e.g., Picman 1988, Yahner and Morrell 1991, Burke *et al.* 2004; but see Gotmark *et al.* 1990, Wilson, *et al.* 1998) and thus the positioning of their artificial nests are a compromise between the breeding densities of their selected species. Artificial nests are often set out in grid-patterns, (Rudnický and Hunter 1993) or transects (Bergin *et al.* 1997) and are usually stratified between habitats, ecotones or roadsides. Unless eggs are placed in disused natural nests, (Ortega *et al.* 1998; Faaborg 2004) or nests are distributed according to the density of the target species, density-dependent effects of nest predation, which have been demonstrated in other studies, (Reitsma 1992, Lariviere and Messier 1998, Schmidt and Whelan 1999, MacDonald and Bolton 2008; but see O'Reilly and Hannon 1989; Ackerman, Blackmer and Eadie 2004) may affect predation rates.

For example, aggregated nests might be located more easily and predated more quickly than dispersed nests. Aggregated artificial nests of new Holland honeyeaters (*Phylidonyris novaehollandiae*) suffered more predation than dispersed nests (Major *et al.* (1994). Nearest-neighbour nests were predated within one hour of each other and if eggs are aggregated they are predated rapidly (Bayne *et al.* 1997b; Chase 2002, but see Reitsma 1992). Crows (corvus) have been shown to locate more artificial nests when nests were aggregated, thus supporting the nearest-neighbour effect (O'Reilly and Hannon 1989, Sugden and Beyersbergen 1986, 1987, and Lariviere and Messier 1998).

Nesting densities in artificial experiments tend to be artificially high and this might be important when predator home ranges are large. For example, predators with large home ranges e.g., carrion crow, (*Corvus corone*) are able to exploit heterogeneity in nest density, whereby detecting high nest densities and modifying their search strategy accordingly (Schmidt and Whelan 1999). Predators with small home ranges (e.g., 1-2 ha or smaller) will encounter too few nests to detect changes in nest densities (Schmidt and Whelan 1999). One of the major predators of nightjar eggs is thought to be the carrion crow (*C. corone*). A closely related species, the hooded crow *C. cornix*, has been shown to switch to active searching after detecting a certain number of nests within a small area, and within a short duration of time (Sonerud and Fjeld 1984). If the encounter rate with prey dropped below a certain threshold, the crows stopped actively searching. This has interesting implications for the structuring of avian nesting assemblages and the nesting density of individual species. Nests at such artificially high densities may make active searching energetically profitable, but natural nesting densities should preclude this searching mode. For example, independently of any effect of food quality or quantity on habitat selection it may be profitable to defend large territories to reduce such density effects of predation (Martin 1998). Knapton, (1979) noted that the clay-coloured sparrows (*Spizella pallida*) nested at low densities to reduce predation risk. Finally, in contrast, a comparison between artificial and natural duck nests provided no evidence of density dependent predation regardless of spatial scale (Ackerman, Blackmer and Eadie 2004). The authors

concluded that geographical variation in the composition of the predator community and the availability of alternative prey were important factors in predation rates (Ackerman, *et al.* 2004).

4.1.7 Nest concealment

Individuals may benefit by keeping potential predators in view, and selection of nest site may be a trade-off between concealment and visibility (Gotmark *et al.* 1995). They showed that for artificial nests, the risk of predation decreased when nests were afforded greater concealment. However, the song thrushes (*Turdus philomelos*) in their study selected vegetation with intermediate concealment from the range of concealment available. Interestingly, the proportion of destroyed natural nests was not related to degree of nest concealment. They concluded that their findings supported the trade-off hypothesis. Burhans and Thompson (1998) found that nests lost concealment with time but that predation did not increase. However, they showed that numerous studies had not considered this factor and only measured concealment after the experiment had finished. The benefits of visibility are that incubating or brooding parents can monitor potential threats and escape capture by fleeing at an optimal distance from the predators (or disturbance) or remain at nest if the threat can be monitored without unnecessarily disclosing the nest.

To summarise, the main reasons for questioning the validity of experiments using artificial nests to assess predation include: (i) lack of natural and artificial nest controls: e.g., appropriateness of egg choice in terms of size, colour and number, novel odours, egg laying date, nest site choice and so on; (ii) disparities in predation rates between artificial and natural nests, between and within studies; (iii) inconclusive identification of nest predators; (iv) assumptions that predators respond equivocally to artificial and natural nests; (v) effects of varying degrees of fragmentation - i.e. edge, patch, landscape; (vi) density effects; (vii) disregard for the effects of researcher activity (on focal species and predators of that species); (viii) poor ecological understanding of focal species, and, (ix)

multi-species experiments.

In a review of studies using artificial nests, Major and Kendal (1996) concluded that future experiments be required to include; (i) a *natural control*, i.e. real nests of the species under study, monitored and treated in the same way as the artificial control; (ii) an *artificial control*, i.e. artificial nests differing from the natural nest only on account of being artificial, but differing from the artificial treatment solely by the variable under observation; (iii) the *artificial treatment*, i.e. artificial nests constructed to examine the effect of a single variable, (e.g., nest visitation). The following experiment aims to consider and control for these potential sources of bias by assessing the effects of researcher activity on nesting success in relation to habitat selection in two populations of nightjars nesting in habitat mosaics of commercial forestry and heathland.

4.1.8 Nest visitation and predation

The relationship between researcher activity and incidence of predation on study organisms is a long-standing concern (Johnson 1938) and remained largely unstudied until the advent of new technologies to remotely monitor nests (e.g., miniature video cameras, MacDonald and Bolton 2008). Until such studies were performed most researchers assumed that nest predation increases with visitation and this was the finding of Gotmark's (1992) review on the subject. However, a growing body of research has begun to consider this experimentally with alternative ways (to Mayfield 1975) of statistically estimating nest success (e.g., Rotella, Taper, and Hansen 2000; Schafer 2004). In a meta-analysis of 18 experimental studies involving 25 bird species Ibáñez-Álamo, Sanllorente and Soler, (2011) found little evidence for an effect of researcher activity on the incidence of nest predation rates. However, this varied between studies with passerines, coastal areas and ground nesting species showing an increase in nest survival with elevated visitation rates. Intriguingly, they found positive effects on nest success in studies that used varying frequency of visitation compared with studies that used visit/non-visit methodology. They concluded that differences in nest survival rates among orders and

guilds could be due to different nest predator communities. Moreover, sensitivity of predatory species and avoidance of the researcher activity may have resulted in these positive effects (Weidinger 2009, Francis, *et al.* 2012).

Conclusive evidence for an effect of visitation on nest survival was shown for visited nests of yellow-billed divers (*Gavia adamsii*) and pacific divers (*Gavia pacifica*), which were 30% less successful than unvisited nests (Uher-Koch, Schmutz and Wright 2015) and frequently disturbed pin-tailed sandgrouse (*Pterocles alchata*) experienced low breeding success (19%) (Mougeot *et al.* 2014) In contrast, there was no effect of researcher activity on lark sparrow (*Chondestes grammacus*) nest survival (Martin *et al.* 2011, Jacobsen *et al.* 2011). Finally, predation rates between frequently visited and infrequently visited finch-lark, (*Eremopserix verticalis* and *E. australis*) nests were no different, indicating that subsequent visits had no cumulative effect on predation (Lloyd *et al.* (2000).

Natural and artificial nests might be predated at different rates in relation to different levels of disturbance. Increased levels of predation were caused by multiple visits to both real and artificial nests resulted in similar predation for real and artificial nests visited at varying rates (Bowen *et al.* 1976, Gottfried and Thompson 1978, Erikstad *et al.* 1982, Galbraith 1987, MacIvor *et al.* 1990, Major 1990, Berg 1992, Mankin and Warner 1992, and Esler and Grand 1993). In contrast Berg (1996) found that the artificial nests in his study experienced almost 80% more predation than natural nests. He suspected that because he had visited the artificial nests repeatedly, but had monitored the natural nests remotely that predation was human induced. Willow ptarmigan (*Lagopus lagopus*) nests experienced 80% predation compared to only 45% of the artificial nests. Interestingly, natural nests were visited more often than artificial ones but the researchers felt that this didn't account for the difference because predation remained the same in weeks 1 and 2, although nest visits declined by half in the second week. However, predators may have learned to follow the paths (whether mechanical, visual, or indeed olfactory) created by the visits and this prolonged the period of predation (O'Reilly and Hannon (1989).

Not only might visitation result in higher predation but it might lead to more rapid predation dependent upon its intensity. For example, higher rates of predation occurred at artificial nests, caused by researcher visits, where 80% of all predation occurred less than 1 hour after observer's left nests (Bayne and Hobson 1997).

4.1.9 Controlling for the effects of researcher activity

To the authors knowledge few studies have adequately controlled for the effect of researcher activity when aiming to compare predation rates between artificial and natural nests. It is essential to be able to measure this effect because the majority studies rely on close observation of their artificial nests. However, in so doing, they may actually affect the rate of predation. Unless studies acknowledge this potential 'observer effect' their results should be regarded with some scepticism. Furthermore, lack of understanding of the behavioural ecology of the target species, may allow subtle side effects of human visitation to be overlooked.

As Major and Kendal (1996) highlight, it is likely that specific sensory cues are given by both natural and artificial nests and that predators may only be able to identify certain ones. Further, even though researchers might attempt to control some of the sensory cues they may actually provide more cues to predators at artificial nests and thus they may experience higher predation rates accordingly. For example, Donalaty and Henke, (2001) studied the effects of scent masking methods to test whether these had an effect on survival of artificial nests. They found no difference in predation rate between 'human scent masked by a neutralizing agent', 'human scent masked by dog scent', and 'human scent as a control' concluding that olfactory predators were capable of locating nests despite attempts to conceal scent trails. Indeed, so-called fox repellent actually attracted foxes to treated duck nests which suffered a 50% predation rate in contrast to the untreated nests which only experienced a predation rate of 9% (Hammond and Forward 1956). The assumption that human scent attracts predators is flawed and mammalian

predators actually avoided artificial nests because they initially smell of humans (Fjeld and Sonerud 1984).

Attempting to provide natural sensory cues at artificial nests has also been employed. The use of diluted chicken faeces sprayed at the entrance to artificial wheatear nests had no effect on predation (Part and Wretenberg 2002). However other studies have shown that depositing the faeces of the prey species at artificial nests increased their likelihood of predation. This is because mallard *Anas platyrhynchos* excrete at the nest as an antipredator response and repeated human visits may result in predators being attracted to the scent of the duck excreta and hence lead to predation of the nest (Olson *et al.* 1998, Clark *et al.* 1997).

Researchers have attempted to avoid being detected by diurnal visual predators by setting out their nests during the night, (Sonerud and Fjeld 1987) or by visiting non-nest patches as well as artificial nests to confuse predators, (Sieving 1992) but without providing evidence of an effect.

In summary, the possible mechanisms of 'observer effect' that may lead to increased predation are, (i) increased exposure of eggs/young and possible increase in begging calls, (ii) invoking parents to perform distraction displays etc. which may attract predators, (iii) creation of paths to nests, (iv) leaving a scent-trail, (v) marking nests, (vi) predators associating human presence with food (vii) destruction of foliage around the nest thereby increasing its visibility.

4.1.10 THIS STUDY

The following study took micro and macrohabitat measurements of nightjars nesting in commercial pine plantations from Chapter 3 and used these to construct artificial nests on five different habitat types, typically used by nesting nightjars. The habitat variables measured were the same as the previous study, but in the analysis, emphasis is placed on

the effects of territory morphology and habitat structure on predation rate in relation to researcher activity. Key territory and nest site variables included: song territory area (ha), compactness ratio, habitat type, distance to habitat edge (m), type of habitat edge (soft or hard), vegetation density and height around nest, number of alternative nest sites and in addition visit status (visited or unvisited).

The aims of this study are, (i) to use the habitat requirements of two populations of nightjar breeding in commercial pine plantations to generate artificial nests and territories, (ii) to examine the relationship between nest visitation and incidence of predation, using artificial nests, (iii) to determine whether nest site choice affects the rate of predation, (iv) to compare the predation rates between natural and artificial nests in different habitat categories, and (v) to identify nest predators. Numerous measures were taken to overcome the potential sources of bias, which have been experienced by other researchers conducting experiments using artificial nests. These include, using artificial eggs and nests that 'matched' those of nightjars to monitor predation of actual nightjar nests in terms of egg size and patterning and vegetation variables around nests.

4.2 METHOD

Study sites. See Chapter Three for details about the location and timing of the studies.

38 nests were located (Nottingham, n=21 (12 of which were radio tagged), Dorset, n=17 (9 of which were radio tagged)). See section 3.3.2 Population census and breeding status in Chapter 3 for more details.

Nightjars, especially incubating birds, will sit tightly and usually only flush when approached rapidly or within <3-4m. Measures were taken to minimise disturbance to incubating birds. These included visiting the nests every five days and remotely monitoring their progress using either a radio receiver to determine if the female was still sitting on the nest or by using binoculars and observing from distance where applicable. It is difficult to determine if the female is incubating without flushing her but one can see if she is

brooding because nightjars do not remove the eggshell once a chick has hatched and chicks defecate within the nest patch (Cramp 1985).

4.2.1 Egg laying period

The artificial nests were deployed to coincide with the second full moon of the typical nightjar breeding season in an attempt to eliminate this potential source of bias. However, the full clutch was provided at the start. This is in contrast to the asynchronised egg laying of the nightjar, which can be 36-48 hours between the laying of the first and second egg, in the clutch.

4.2.2 Egg characteristics

Two types of artificial nest were constructed; one containing both a quail egg, and a plasticine replica nightjar egg, and another consisting of two quail eggs to control for the novel odour of plasticine which might attract olfactory predators. Plasticine eggs were used so that they could record the imprints of the beaks, teeth, or claws of predators. The marked eggs were compared to equivalent marks left on plasticine eggs by museum specimens of the suspected predators.

In terms of appearance, the degree to which the quail and plasticine eggs approximated to those of the nightjar is detailed in Table 4.1. The quail and the plasticine egg resembled characteristics of nightjar eggs with regard to size. Clutch size also mirrored that of the host species, as two eggs were placed in each nest. Both colouration and patterning have been shown to affect predation rates between nests, and satisfied the requirements set out by Major and Kendal (1996). All the quail eggs were bought fresh from a local farm and were placed in the field within 2 days of purchase. The eggs were rinsed with rainwater and rubber gloves were worn to handle eggs intended for “unvisited” nests. It was regarded as equally important that the plasticine egg approximate as much with quail egg as with the nightjar egg.

Variable	Egg characteristics		
	Nightjar	Quail	Plasticine
Egg Width (mm) ^a	22-24	24-26	24
Egg Length ^b	30-34	31-34	32
Egg Colour ^c	grey-white/cream	white/cream	white/cream
Egg Patterning ^c	spots-beige/dark brown scrawls-grey/brown	spots/blotches-dark brown/yellowish	spots/blotches-dark brown/ beige scrawls-grey/brown
Egg texture ^c	smooth/fairly glossy	smooth/fairly glossy	smooth/matt
Egg freshness ^d	N/A	<4 days	N/A
Clutch size ^e	2	2 or 1	1

Table 4.1 Measurements and characteristics of nightjar, quail and plasticine eggs. ^a Appropriate if within 25% difference in egg width given by Cleere (1998) as specified by Major and Kendal (1996). ^b Appropriate if within 25% difference in egg length given by Cleere (1998). ^c Appropriate if they comply with the description given by Cleere (1998). ^d Appropriate if fresh. ^e Appropriate if within range specified by Cleere (1998).

4.2.3 Nest site choice

Appropriateness of nest site choice was determined by taking measurements from the nightjar nests and territories, (see Results section, Chapter 3) and statistical analysis ensured that the artificial nest sites possessed similar vegetation attributes (Table 3.3 Chapter 3). These included microhabitat measurements of vegetation density above and surrounding the nest, vegetation height, and larger scale attributes including distance to edge, edge type, area, and compactness ratio (Figure 4.1).

The artificial nests were constructed on sites that were not occupied by nightjars to avoid creating an artificially high density of nests for potential predators. One hundred nests were distributed equally (20 in each habitat) in accordance with habitats occupied by nightjars. Those included unplanted clear fells dominated by grass or bracken, conifer plantings <4 years, plantations from 4-9 years old, and heathland. Although the number of the artificial nests was equal between habitats the density reflected the relative nesting density of nightjars which varied between habitats. This was possible because of the small

size of the nightjar populations and the amount of unoccupied habitat. Half (10) of the artificial nests in each habitat were visited, the other half were not. Nests that were 'unvisited' were inspected for suitability 10 days prior to the start of the experiment to allow any physical or olfactory cues to ameliorate and the appropriate habitat measurements were taken (Figure 4.1).

4.2.4 Artificial nest, visitation and construction

4.2.4.i 'Unvisited nests'

The title, 'unvisited' is merely a term to describe how the nest is treated experimentally, post construction. Thus, unvisited artificial nests (i.e. nests that were remotely monitored after their construction) were built by walking to within 5m of the nest patch wearing thigh length rubber waders. The waders had been left in a forest glade for 2 weeks prior to being used in an attempt to disguise any human scent. The eggs were then placed into a container attached to the end of a 5m pole, similar to the golf-ball retriever method used by MacIvor *et al.* (1990), and then gently rolled into the nest patch. A different route was taken when leaving the nest area to avoid the creation of a path (Figure 4.1).

4.2.4.ii Visited nests

In contrast, at visited nests, the researcher meandered through the habitat as if looking for a nest. On 'discovery' of the nest site a three-dimensional model of a female nightjar in flight was catapulted out of the nest patch and a tape recording of a distressed adult performing an injury feigning display was played for ~8 minutes, (the length of time it would normally take to record nest site characteristics for a newly discovered nest) with a three-dimensional model of a nightjar perched near the tape recorder, in an attempt to mimic the finding of a nightjar nest (Figure 4.1). It should be noted that incubating nightjar typically fly away if flushed but the aim was to provide predators with the maximum number of 'natural' cues.

The nest site characteristics were recorded in the same way as a real nest. The eggs were

measured, weighed, and placed in the nest. If a plasticine egg was to be left, it was fixed to the ground from beneath with a length of wire to reduce the risk of a predator taking it away. The nest patch was then photographed. Nest site and habitat measurements were taken in accordance with the methods in Chapter 3. When constructing both visited and unvisited nests, evidence of the presence of potential predators was recorded (Figure 4.1).

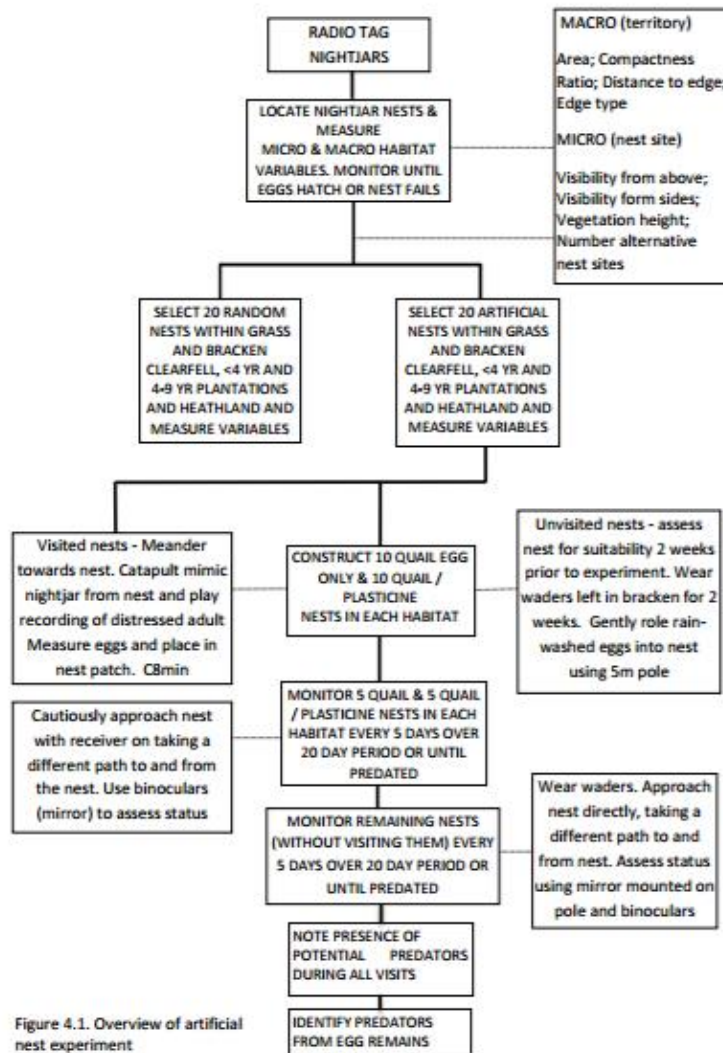
4.2.4. iii Nest monitoring

In accordance with the 5 day check to monitor nightjar nests the status of both sets of artificial nests were checked every 5 days. Nests were monitored over a 20 day period in an attempt to approximate the 18 day, sometimes 21 day, incubation period of the nightjar. At visited nests, the nest patch was approached cautiously and the receiver was turned on, as if trying to locate the radio tag. The status of the nest could then be assessed with the use of binoculars. However, some nests required the use of a small mirror mounted on a 5m pole, with which the eggs could be inspected. Unvisited nests were treated similarly to the visited nests, except the receiver was not used and waders were worn when walking towards the nest area (Figure 4.1). Nests that were concealed had to be inspected from within 4m but this never involved actually standing in the nest site. If a nest was predated between the 5 day checks its survival was estimated at half way between the check dates (Mayfield 1975). If a nightjar nest was successful it was estimated to have survived for 20 days, regardless of the date the nest was discovered.

4.2.5 Statistical analysis

Predation was measured in 2 ways: predation rate, the number of nests predated and nest survival, the rate at which nests were depredated. Generalized Linear Models (GLZMs), Statistica version 11 measured predation and nest survival in relation to the different treatments, egg type, visit status and the ecological characteristics of each habitat looking for main effects and interactions. Further analyses were used to interpret the direction of any main effects and interactions from the GLZMs. Initial analyses consisted of statistical tests of whether predation of nightjar and artificial nests was equal.

These include χ^2 , Pearson's correlation, independent t-test and one-way ANOVA and were all completed using SPSS version 21.



4.3 RESULTS

4.3.1 Comparison between attributes of nightjar and artificial nest sites and territories

In contrast to randomly selected nest sites (Chapter 3), there were no significant differences between nightjar and artificial nests in the different habitat categories for, alternative nest sites, vegetation height (m), vegetation cover from above, vegetation cover from the sides, distance to edge (m), edge type, area (ha) and compactness (Table 4.2).

Table 4.2 Independent samples t-tests for habitat variables for nightjar (n=38) versus artificial nest sites (n=100) in the 5 habitat categories.

* denotes significant difference. In all cases df=1.

	Grass clearfell				Bracken clearfell				<4 year plantations				4-9 Plantations				Heathland			
	t	p	Mean diff	SE	t	p	Mean diff	SE	t	p	Mean diff	SE	t	p	Mean diff	SE	t	p	Mean diff	SE
Alternative nest sites	-0.63	0.54	-1.12	1.78	0.04	0.97	0.08	2.07	-0.44	0.67	-0.55	1.27	-0.46	0.65	-0.61	1.34	-0.53	0.60	-0.90	1.69
Vegetation height (m)	0.72	0.48	0.05	0.07	0.67	0.51	0.09	0.14	-0.63	0.54	-0.04	0.07	-0.28	0.78	-0.03	0.12	-0.12	0.91	-0.01	0.07
Vegetation cover from above	-0.21	0.84	-0.01	0.04	-0.03	0.98	0.00	0.06	-0.30	0.76	-0.01	0.03	-0.11	0.92	-0.01	0.06	0.05	0.96	0.00	0.04
Vegetation cover from the sides	-0.77	0.45	-0.03	0.03	0.17	0.87	0.01	0.06	-0.38	0.71	-0.01	0.03	-0.33	0.74	-0.01	0.04	0.38	0.71	0.02	0.05
Distance to edge (m)	-0.28	0.78	-0.88	3.16	0.10	0.92	0.38	3.73	0.20	0.84	0.61	3.01	0.51	0.62	1.54	3.03	-0.16	0.87	-0.55	3.43
Area (ha)	-0.29	0.77	-0.16	0.53	-0.28	0.78	-0.26	0.93	0.42	0.68	0.35	0.84	0.85	0.40	0.28	0.33	0.29	0.78	0.09	0.31
Compactness ratio	0.18	0.86	0.01	0.05	-0.02	0.98	0.00	0.04	0.14	0.89	0.00	0.03	0.17	0.87	0.01	0.04	0.06	0.95	0.00	0.03

4.3.2 Predation of nightjar versus artificial nests

Overall predation of nightjar nests (16 of 38; 42%) was not significantly different from quail only nests (22 of 50; 44%) and quail/plasticine nests (23 of 50; 46%) ($\chi^2=0.134$, $df=2$, $p=0.935$) during the experimental period.

Nightjar and artificial nests elicited a similar response from predators (daily survival rate (DSR - Mayfield 1975), nightjar nests - 0.955 and artificial nests - 0.963). When nest survival is analysed by habitat type there are good approximations between the DSR for nightjar and artificial nests (Table 4.3). In three habitats, grass clearfells, bracken clearfells and <4 year plantations nightjar nesting success was lower than artificial nests, in 4-9 plantations, daily survival was identical and in heathland, nightjars have higher daily survival. When nest predation is based upon egg type, i.e. real, quail or plasticine, it is apparent that of 74 nightjar eggs, 31 (41.8%) were predated, of the 150 quail eggs, 63 (41.3%) were depredated, and of the 50 plasticine eggs, 24 (48%) were depredated ($\chi^2=0.06$, $df=2$, $p>0.993$). In just over 10% of the artificial nests only one egg was predated and in 2 of the nightjars' nests only 1 egg had been laid and one nest was predated and the other abandoned.

Habitat	Nest	Failed during incubation (n)	Exposure days (n)	SD	Daily survival rate Mayfield (DSR)
Grass clearfell	Nightjar	4	61	4.71	0.934
	Artificial	13	207.5	7.71	0.937
Bracken clearfell	Nightjar	5	55.5	4.16	0.91
	Artificial	16	220	5.98	0.927
<4 year plantation	Nightjar	5	100	3.96	0.95
	Artificial	9	282.5	6.94	0.968
4-9 plantation	Nightjar	1	124.5	4.15	0.992
	Artificial	3	382.5	2.84	0.992
Heathland	Nightjar	1	108.5	4.37	0.991
	Artificial	4	345	5.72	0.988

Table 4.3 Daily survival rate of nightjar and artificial nests in 5 different habitat categories. Exposure days represent the total number of days that all nests survived for in that habitat. DSR = (Exposure Days - Number of failed nests)/Exposure Days. (Mayfield 1975).

4.3.3 Predator identification

Nightjar and artificial nests were depredated by different predator assemblages and at different rates. All but four nightjar nests were depredated by birds and triangular punctures in egg shell remains suggest that carrion crow (*Corvus corone*) was responsible. A green woodpecker (*Picus viridis*), was flushed from the site of a nest where the eggs had been predated by a bird and marking on the shells were comparable to those of green woodpecker. Nightjar eggs were removed from four nests and the nest areas had been dug in two of these. The flight feathers and retrices from a female nightjar were found near the nest scrape and their shafts were broken suggesting fox (*Vulpus vulpus*) was the predator.

Predator	Nightjar	Quail	Plasticine
<i>Corvus corvus</i>	17	39	7
<i>Garullus garullus</i>		9	3
<i>Pica pica</i>		4	2
<i>Picus viridis</i>	1		
<i>Dendrocopos major</i>			1
<i>Vulpus vulpus</i>	9	2	2
<i>Erinaceus europaeus</i>			2
<i>Mustela erminea</i>			2
<i>M. nivalis</i>			1
<i>Apodemus sylvaticus</i>		8	
<i>Rattus norvegicus</i>			3
<i>Sciurus carolinensis</i>			2
<i>Vipera berus</i>		2	
unidentified	4	11	10

Table 4.4. Predation of nightjar, quail and plasticine eggs by predator species. Nests containing a single quail and plasticine egg experienced greater mammalian predation than other nests. In the majority of depredation rodents had gnawed the plasticine egg. Peak predation for all nest types occurred between the 5 and 10 day check but there was a more rapid predatory response to nests containing quail and plasticine eggs at the first 5 day check. In 22% of depredation events the predator could not be identified to species either because the eggs had been removed or eggs had been predated by multiple predators (n=11).

When predation was based upon nightjar only nests, there was a significant difference in the nesting success between habitats (ANOVA, F=4.14, df=4, p=0.008). Post hoc Tukey test

showed that birds nesting in heathland (DSR 0.991) and 4-9 year plantations (DSR 0.992) had a higher nest success than birds nesting in bracken dominated clearfells ($p=0.035$ and $p=0.025$ respectively) and grass clearfells ($p=0.048$ and $p=0.04$) (Table 4.3 Appendix A Figure S4.1). When predation is based upon the artificial nests there is also a significant difference in nest success between the habitats (ANOVA, $F=8.11$, $df=4$, $p<0.001$). Birds nesting in heathland (DSR 0.988) and 4-9 year plantations (DSR 0.992) had higher nest success than birds nesting in bracken and grass dominated clearfells (bracken clearfell nests $p<0.001$; grass clearfell nests $p=0.014$; bracken clearfell nests $p<0.001$; grass clearfell nests $p=0.005$ respectively) (Table 4.3 and Figure S4.2).

4.3.4 Temporal effects on nest concealment

Mean nest concealment of the 38 natural nests, i.e. the amount of cover from above, vegetation density and height had increased on average 18% by the end of the 20 day check. It changed the least at 6% in heathland, 11% for 4-9 year plantations, 16.5% grass clearfell, 19% for <4 year plantations but by 27% for bracken clearfells. In the latter habitat, foxglove and bracken were probably responsible for the greater change. The figures were very similar for artificial nests. We did not include this in the analyses but will refer to it in the discussion.

4.3.8 Evaluation of variables

Generalized linear models (GLZMs) were used to evaluate the relative importance of the habitat variables, 'nest visitation' and 'egg type' on nest predation. Binomial distribution was used with the logit link function and quick specs dialog specification method. Logit is the default link function for binary data, i.e. predated/unpredated. We also ran the analysis with 'nest survival' as the dependent variable and we used the link function cumulative logit for the multinomial data distribution. We analysed the data using the best subsets routine to identify the top 20 models (from a maximum of 5000), by AIC criteria. In all cases AIC values were similar for the best 10 models (AIC values varying by less than 2), indicating that the models were approximately equivalent in their estimation

of the variance. We then used the model from this set with the highest number of independent variables.

Interaction terms between independent variables could not be computed because the distribution of categories was excessively uneven between variables (e.g., egg type 1 (nightjar) only turned up with visit status 1 (visited)). Hence, we present models with no interaction terms here. We did though check for the suitability of interaction terms in a set of simpler two-way analyses. Interaction terms were never present in the best subset(s), and were non-significant in models anyway.

4.3.9 Predation rate

The dependent variable was predation rate: categorical variables included habitat, egg type, edge type and visit status; continuous variables were number of alternative nest sites, distance to edge, area, compactness ratio and vegetation density. Vegetation height and cover were correlated with vegetation density and the model would not run with their inclusion so they were omitted.

	df	Wald Chi Square	p
Intercept	1	0.00052	0.982
Edge	1	4.34779	0.037*
Area	1	0.67232	0.412
Distance to edge	1	2.87654	0.091
C-ratio	1	2.61882	0.106
Vegetation density	1	1.61629	0.203
Habitat	4	18.61207	0.001*
Visit status	1	4.07622	0.044*
Alternative nest sites	15	18.92510	0.217

Table 4.5 GLZM analysis of nest predation for nightjar and artificial nests in relation to various habitat variables and visit status.

Habitat, edge and visit status were the best predictors of predation (Table 4.5). When nightjar and artificial nests were pooled there was a significant overall difference in the amount of predation in the different habitats (ANOVA, $F=12.53$, $df=4$, $p<0.001$). Nests on grass clearfells experienced significantly higher predation than those on 4-9 year plantations ($p<0.001$) and heathland ($p=0.001$). Those on bracken clearfells experienced significantly more than nests on <4 year plantations ($p=0.047$), 4-9 year plantations ($p<0.001$) and heathland ($p<0.001$), and those on <4 year plantations experienced significantly higher predation than nests in 4-9 year plantations ($p=0.023$) (Figure S4.3).

Analysis of mean nest predation in relation to edge type showed a near to significant difference for nightjars - (T-test, $t=1.83$, $df=1$, $p=0.07$), (Fig. S4.4) and a significant difference for artificial - (T-test, $t=2.74$, $df=1$, $p=0.007$), (Fig. S4.5). In both cases nests adjacent to hard edges were more likely to be depredated. In total 98 nests occurred adjacent to soft edges and of these 35 were depredated and 63 were not. 40 nests were adjacent to hard edges and of these 26 were depredated and 14 were not ($\chi^2=9.88$, $df=1$, $p=0.002$). This also varied by habitat but samples in categories were too small to allow statistical analysis.

Although there was a significant effect of visit status on total nest predation further analysis found no significant difference overall (T-test, $t=1.69$, $df=1$, $p=0.305$) or, when analysis was based on types of nest (ANOVA, $F=0.66$, $df=2$, $p=0.936$) but there was a tendency for nests containing a plasticine egg to experience less predation if visited (Figure S4.6). Significantly, the main effect of visit status on predation was caused by the increased success of visited artificial nests on bracken clearfells and <4 year plantations. Nightjar nest predation was not significantly different to artificial nest predation with regard to visit status so we can conclude that visit status had an equal effect on both nest types.

When the analysis is run but this time replacing habitat with nest type we get the following output.

	df	Wald Chi square	p
Intercept	1	0.00065	0.979
Vegetation density	1	1.33501	0.248
Edge	1	4.97817	0.026*
Distance to edge	1	3.11785	0.084
C-ratio	1	2.27945	0.131
Nest type	9	22.32575	0.008*
Alternative nest sites	15	19.38586	0.197
Visit status	1	4.96270	0.026*

Table 4.6 GLZM analysis of nest predation for nightjar and artificial nests in relation to habitat variables and visit status but replacing habitat with nest type * denotes significant effect or interaction. Nest type relates to nightjar or artificial nests in the 5 habitat categories.

Edge and visit status remain significant, and nest type becomes significant (Table 4.6). Analysis shows that the significant effect of nest type is caused by the higher predation rates of both nightjar and artificial nests in bracken and grass clearfells (ANOVA, $F=5.45$, $df=9$, $p<0.001$). Both nightjar and artificial nests on grass and bracken dominated unplanted clearfells experienced the highest predation, and both nightjar and artificial nests on heathland and plantations 4-9yrs experienced the lowest. There were no significant differences between predation of nightjar and artificial nests within each habitat (grass clearfell - $p=0.998$, bracken clearfell - $p=0.992$, <4 year plantation - $p=0.89$, 4-9 year plantations - $p=0.99$, heathland - $p=0.98$).

Due to the number of categories in some variables and the small size of samples, coupled with the uneven distribution of data, a number of sub analyses were run in order to establish if there were any significant interactions between key predictors. The key point

here is that there were no significant interactions between habitat and egg type (Table 4.7) or habitat and visit status (Table 4.8, and Figure 4.2).

	Df	Wald Chi-square	p
Intercept	1	0.001	0.994
Habitat	4	18.86	0.001*
Egg type	2	0.003	0.998
Habitat*Egg type	8	4.273	0.832

Table 4.7 GLZM analysis of nest predation for nightjar and artificial nests in relation to habitat and egg type and their interaction

	Df	Wald Chi-square	p
Intercept	1	0.867	0.352
Habitat	4	28.29	0.001*
Visit status	1	0.66769	0.414
Habitat*Visit status	4	3.95288	0.412

Table 4.8 GLZM analysis of nest predation for nightjar and artificial nests in relation to habitat variables and visit status. * denotes significant effect or interaction.

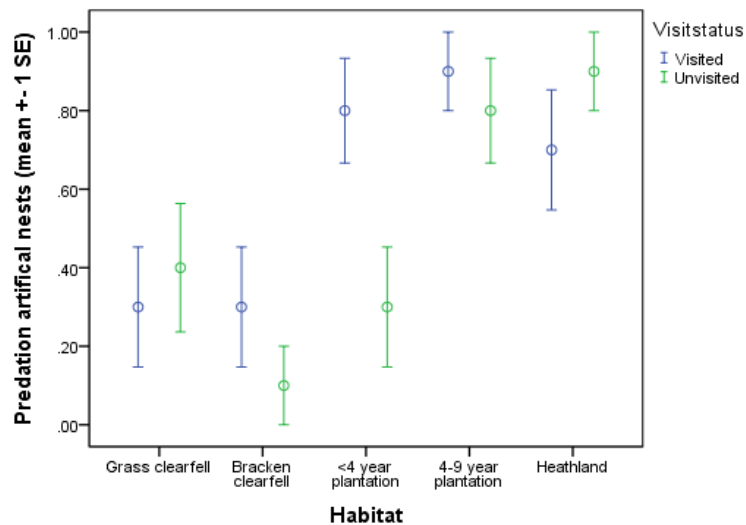


Figure 4.2 Comparison between mean predation rates of artificial nests in different habitat categories based upon visit status ($\pm 1SE$).

4.3.10 Nest survival

In these analyses, we replaced predation with nest survival as the dependent variable and we included the maximum number of main effects, removing only significantly correlated predictors. Vegetation height and vegetation cover from above correlated with vegetation density so these were removed. Models would not run when nest type was included.

	Df	Wald Chi-square	p
Intercept	1	3.813059	0.051
Vegetation density	1	4.529401	0.033*
C-ratio	1	4.592758	0.032*
Area	1	5.654919	0.017*
Distance to edge	1	3.610456	0.074
Edge	1	1.190407	0.026*

Table 4.9 GLZM analysis of nest survival (days) for nightjar and artificial nests in relation to various habitat variables. * denotes significant effect or interaction.

Area, edge, compactness ratio and vegetation density, were the best predictors of nest survival within the analysis with the maximum number of variables (Table 4.9). Nest survival decreased with territory area ($r=-.282$, $n=138$, $p=0.001$) because the majority of successful nests were in heathland and 4-9 year plantations and nightjars nesting in these habitats occupied smaller territories. It also decreased with edge type (T-test, $t=3.69$, $df=1$, $p=0.001$) wherein nests adjacent to hard edges were predated more rapidly (Figure S4.7). In contrast, nest survival increased in tandem with vegetation density ($r=.294$, $p<0.001$, $n=138$) and compactness ratio ($r=.261$, $p=0.02$, $n=138$).

To look for interactions a subset of factors from the most significant model were run (due to data constraints highlighted above). The model would not run with interactions between egg type and habitat or egg type and visit status.

	Df	Wald Chi-square	p
Intercept	1	11.18547	0.001
Visit status	1	0.02123	0.884
Habitat	4	14.27259	0.007*
Visit status*Habitat	4	6.55624	0.161

Table 4.10 GLZM analysis of nest survival (days) for nightjar and artificial nests in relation to habitat and visit status and their interaction. * denotes significant effect or interaction.

In this model with interactions habitat was the only factor that systematically explained the variation in nest survival (Table 4.10). Notably, there were no significant interactions between habitat and visit status (Table 4.10, Figure 4.3). In terms of nest survival and habitat, nightjar and artificial nests in heathland and 4-9 year plantations survived for longer than nests in grass clearfell ($p<0.001$ and $p<0.001$), bracken clearfell ($p<0.001$ and $p<0.001$) and nests in 4-9 year plantations survived longer than those in <4 year plantations ($p=0.008$) (Figure S4.8).

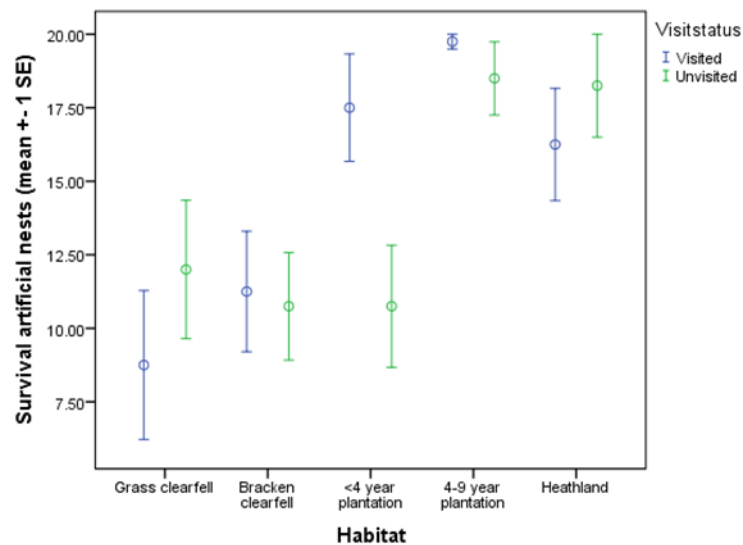


Figure 4.3 Comparison between nest survival (days) of nightjar and artificial nests in different habitat categories in relation to visit status

4.4 DISCUSSION

4.4.1 Effects of habitat selection and researcher activity

The aim of the experiment was to measure the effects of habitat selection and researcher activity on the nesting success of two populations of plantation nesting nightjars, using artificial nests. The major findings of the study are outlined below. Depredation on artificial nests was not significantly different to nightjar nests, suggesting that predators were responding to them equivocally. However, predation of nightjar and quail nests was mainly avian, whereas mammals accounted for the majority predation of artificial nests containing a plasticine egg. Nest visitation had a positive effect on artificial nest success in <4 year plantations.

Generalized linear modelling showed that habitat was the single best predictor of variation in depredation in the largest model, along with edge type and visit status but there were no interactions. In terms of the different habitats (and nest types) depredation was significantly higher on nests in grass and bracken clearfells, followed by <4 year plantations and lowest in 4-9 year plantations and heathlands. Both nightjar and artificial nests adjacent to hard edges were significantly more likely to be depredated. The main effect of visit status on predation was caused by the increased nest success of visited artificial nests on bracken clearfells and <4 year plantations. Temporal effects of vegetative concealment of nests varied between habitats with bracken clearfell sites accruing the greatest increase in cover. Variation in nest survival (days to predation) was explained by territory area and compactness ratio, edge type, and vegetation density. Nests were depredated more rapidly in large territories and when adjacent to hard edges. In contrast, nest survival increased in tandem with increased vegetation density and territory compactness ratio.

4.4.2 Predation of nightjar versus artificial nests

Predation rates for nightjar nests of 42% were midway between those of other studies - e.g., Murison 2002 - 66% based upon 47 nests and Woodfield and Langston 2004 - 28%

based on 29 nests. Nest success of nightjars at the two localities was comparable to previous and subsequent years so we can conclude that these were typical breeding seasons (BRG 1992-1997, SRG 1984-1994 annual reports). Predation rates for nightjar and artificial nests in different habitats were similar (Figure S4.3) and there was no significant interaction between habitat and egg type (Table 4.7), and this concurs with the minority of studies (e.g., Vander Haegen *et al.* 2002). In contrast, evidence that predation of artificial nests is generally higher than that of natural nests is provided by the majority of studies (MacIvor 1990, Berg 1996, Lindell *et al.* 2004, Batary and Baldi 2005), with only a smaller number finding the opposite (Davison and Bollinger 2000, Thompson and Burhans 2004). Daily survival was also very similar between nightjar and artificial nests in different habitats (Table 4.3 and Figure S4.8). From this we conclude that our artificial nests accurately replicated the ecological characteristics of nightjar nests and therefore careful calibration between a single focal species and artificial nests provides a useful means for understanding predation when species are difficult to study and samples sizes small (Moore and Robinson 2004, Villard and Part 2004).

4.4.3 Predatory responses

Although predation rates and nest survival were similar between nightjar and artificial nests predators were not. Not only were predator assemblages different between the nests, but nest survival was predator specific and eggs within artificial nests were predated differently (Table 4.4). Birds were the principal predator of nightjar eggs and quail eggs whereas artificial nests containing a plasticine egg experienced mainly mammalian predation. Vander Haegen *et al.* (2002) also found similar predation between quail eggs and four passerine species in their study. In other studies using artificial nests avian predation of natural nests was also recorded (e.g., Pasitschniak-Arts and Messier 1996) but not by the majority of studies including Willebrand and Marcstom (1988). They found that mammals were the main predator of Eurasian black grouse (*Teatrao tetrix*) but Fjeld and Sonerud (1984) noted that mammalian predators avoided artificial nests. Storaas (1988) found that birds predated artificial nests more than mammals suggesting

that artificial nests lacked the scent of an incubating adult and were not detected by olfactory predators. The main difference in predatory responses to the artificial nest types might relate to the difference in the activity periods of the visual predators, which are diurnal birds, and the olfactory predators, which are nocturnal mammals.

Although the majority of nest predation occurred within the first 10 days, nests containing both quail and plasticine eggs were predated more rapidly than other nest types and the majority of the predation was mammalian (Table 4.4). Plasticine eggs were predated more than quail eggs. One explanation could be that olfactory predators were attracted to the novel odour of the plasticine (e.g., Rangen, Clarke and Hobson, 2000). Also, small mammals may be able to gnaw plasticine eggs but not the shell of equally sized quail eggs leading to overestimates of predation and this was the finding of a study by Bayne *et al.* (1997). Two, of four Longworth traps baited with cubes of plasticine were visited by Wood mouse (*Apodemis sylvaticus*) so olfactory attraction cannot be ruled out.

The temporal effect of predation on subsequent predation (i.e. a predated nest is subsequently re-predated because additional sensory cues are provided) was not explored in this study because it was not anticipated by the author. Not only does it make the identification of nest predators difficult as demonstrated by Lariviere and Messier (1997) but it may create bias in the assemblage of predators. For example, in 11 instances (18% of predation events) in this experiment, nests were predated by both visual and olfactory predators. If the nest was initially predated by a visual predator, the scent of the predated eggs may have attracted the subsequent predation. Olson and Rohwer (1998) showed that cracked eggs experienced more predation by olfactory predators than un-cracked.

4.4.4 Visit status and predation of nightjar and artificial nests

There was no significant difference in the mean predation rate (Figure S4.6) or nest survival (Figure S4.9) between visited and unvisited nightjar and artificial nests. However, in the GLZM analysis there was a positive effect of nest visitation on predation wherein

visited artificial nests on bracken clearfells and <4 year plantations experienced lower predation than unvisited nests (Tables 4.5 and 4.6). This unexpected result is supported by Weidinger (2009) and Francis *et al.* (2012) who suggested that researcher activity at frequently visited nests disturbs reclusive predators. A meta-analysis by Ibanez-Alamo *et al.* (2012) found that ground nesting birds showed an increase in nest success in conjunction with elevated visitation. Others, including Jacobsen *et al.* (2011) found no effect of researcher activity on the nesting success of lark sparrows (*Chondestes grammacus*). Despite these studies, most others have found a positive relationship between increased nest visitation and increased predation (Mouget *et al.* 2014, Uher-Koch *et al.* 2015, Brian *et al.* 2015 see Gotmark 1992 for a review). For example, O'Reilly and Hannon's (1988) study on Willow Ptarmigan showed that 45% of the artificial nests, and 80% of the natural nests, were predated, concluding that the higher rate of predation of the real nests was attributed to the greater level of visitation they received. Significantly, there were no significant interactions between habitat type and visit status on nest predation (Table 4.8) or nest survival (Table 4.9).

Our findings suggest that visual predators were not using human presence as a cue to search for food (artificial nests) (Gotmark *et al.* (1990), and we conclude the same for nightjar nests. Peak predation of nightjar (and all) nests occurred before the 10 day check and nightjar nests were predated mainly by visual predators (Table 4.4). This might suggest that exposed eggs were rapidly depredated due to their conspicuousness (Stoddard *et al.* 2013). Indeed, eight crow-predated nightjar nests and twenty crow-predated artificial nests were within the home range of six known crow nests (whose territories are approximately 500m²) (Baglioni *et al.* 2002). Other nests, where eggs had been removed were within crow home ranges and the eggs could have been cached (Tinbergen *et al.* 1967). Eleven crow-predated nightjars relocated their second nesting attempt greater than 227m (sd=89.4m) from the first nest site. Although too few nests are available to determine the effects of dispersing (as opposed to non-dispersing), this may suggest that post-predation dispersal is important, and is possibly a function of predator

home-range size. Eight of the second breeding sites were outside the 'normal' crow home range, and another was near the 500m boundary. One was subsequently predated. A study by Powell and Frasch (2000) modelled dispersal patterns in double-brooded songbirds, in relation to predators with different home range sizes. They showed that, post-predation, dispersing birds had higher nesting success than non-dispersers; dispersing beyond the home range of the predator also increased nesting success; and predation early in the nesting cycle and subsequent dispersal, was more beneficial than late predation and dispersal. So, with regard to the nightjar, predation events may create a selective advantage for adults to disperse, and explain their relatively larger song territories in riskier habitats. Predation was highest amongst birds defending the largest territories and therefore territory size might be a function of perceived predation risk (Fontaine and Martin 2006, LaManna *et al.* 2015).

Crows (*Corvus* spp.) locate nests in flight (Dwernychuk and Boag 1972), on foot (Sugden and Beyersbergen 1987), and from perches (Salathé 1987). Although carrion crow *C. corone*, jay (*Garrulus glandarius*) and magpie (*Pica pica*) were observed when 59 of the artificial nests were being constructed, only fourteen (24%, or 31% of predated nests) were predated by corvids. This is despite findings by Croze (1970), and Salathe' (1987) who showed that carrion crows rapidly learned to associate humans with food, returning to search for more (food) up to 2 days after the initial discovery and intensified their search effort when encounter rate with prey reached a certain threshold (Sonerud and Fjeld 1984, Lariviere and Messier 1998). The densities at which nightjars nested in these two study sites (and the density at which artificial nests were distributed) should preclude such active searching. Nonetheless, crows may be more likely to associate human activity with food if that activity occurs suitably close to their nests allowing them sufficient time to learn but this does not appear to be the case for artificial food sources (Salathe'1987). Therefore, nightjar nests within corvid home ranges may be more vulnerable to predation, especially if those nests are disturbed by humans during daylight. Grey squirrel also predated nests and a related species the red squirrel has been shown to learn how to find

bird nests and may also use human activity as a trigger to search for nests (Pelech, Smith and Boutin 2010).

Nightjars are very susceptible to disturbance (Liley and Clarke 2002, 2003, Mursion 2002, Woodfield and Langston 2004, Langston *et al.* 2007, Lowe *et al.* 2014). Liley and Clarke (2003) recorded lower breeding densities of nightjars adjacent to urban development and Mursion (2002) and Langston *et al.* (2007) showed that nest success was significantly lower when nests were close to paths. Woodfield and Langston (2004) and Langston *et al.* (2007) proposed that disturbance to incubating nightjars caused by dogs or people led to greater nest predation and this was exacerbated when vegetative cover was low (Mursion 2002). Mursion (2002) speculated that the main predator was *C. corone*. Finally, Lowe *et al.* (2014) conducted a study on the same Nottinghamshire nightjar population as the present study concluding that the higher nest success of nightjars nesting in the south of the forest was attributable to lower recreational disturbance. Unfortunately, they did not measure any ecological parameters and assumed that nests had similar vegetative cover etc. based upon the age and species classification of the forest coupe the nests were located in. The findings of the present study showed that controlled visitation of artificial nests does not lead to increased nest failure and we conclude the same for nightjar nests. This finding does not echo the sentiments of Gribble who, after working on the 1981 nightjar census, concluded that nightjars were too susceptible to human disturbance to allow further study (Gribble pers. comm). As long as researchers do not cause adults to leave their eggs during daylight and avoid the creation of a path after the initial discovery of the nest, nightjar breeding success is quantifiably unaffected.

Although artificial nests were exposed for the entire experiment and their likelihood of being detected by visual predators was greatly increased (Yahner *et al.* 1989), ~60% were not depredated. Predation rates (Figure S4.3) and nest survival (Figure S4.8) were similar between nightjar and artificial nests in relation to habitat type and predator assemblage (for quail egg only nests). In conclusion, the observation that the visited artificial nests in

two habitat categories were predated less than the 'unvisited' ones, although experimentally conclusive, only in part provides evidence that no observable effect on the reproductive success of the nightjars has been caused by human disturbance. In this experiment, only the incubation period was examined. Continued human visitation of nests is likely to have significant effects during the brooding stage when natural cues - e.g., begging calls, odour of chick faeces etc. are present and olfactory predators might become more important. Indeed, Larsen (1996 unpublished data) found that the majority of predation of nests containing chicks were mammalian (9 from 34 chicks - 26%) and faeces around the nest sites and other signs suggest fox was the predator.

4.4.5 Habitat and nest concealment

There was a non-significant effect of vegetation density on predation rate (Table 4.5 and 4.6) and nest survival (Table 4.9) and the relationship between predation and nest concealment is not straightforward. For example, vegetation density was significantly lower on grass clearfells and <4 year plantations and higher on bracken clearfells (Figure S4.10) but the latter experienced slightly higher predation. Vegetation density was similar between bracken and heathland nests but heathlands had higher nesting success. Finally, vegetation density was highest on 4-9 year plantations but nest success was equally high on heathlands where vegetation density was lower. However, some of the differences in predation are non-significantly different and the general pattern is for nest success to increase with concealment. Murison (2002) and Woodfield and Langston (2004) also found that nightjar nests were significantly more successful in habitats with higher vegetation density. These findings are supported by Sugden and Beyersbergen (1987) who showed that predation increased from 29% to 44% when vegetation height decreased from 50cm to <40cm. Jones and Hungerford (1972) showed that predation of their artificial nests by magpies, *Pica spp.* decreased with increased nest concealment. Brittas and Willebrand (1991) demonstrated no relationship between predation and nest crypsis, in their study on predation of black grouse, (*Lyrurus tetrix*) and Howlett and Stutchbury

(1996) compared nests of hooded warblers (*Setophaga citrina*) with varying vegetative cover and experimental nests lacking cover finding no difference in nest predation.

Indeed, our finding is contrary to the majority of studies (e.g., Gottfried and Thompson 1978, Zanette and Jenkins 2000). The significant finding of this study is that nightjars do not nest in the densest vegetation within their territories, which is not in full agreement with Murrison (2002) and Woodfield and Langston's (2004). Indeed, Woodfield and Langston (2004) also noted that nightjars were more likely to 'flush' (fly from nest) at a greater distance to the source of disturbance if their nest was located in taller vegetation. In the present study, data on flushing distance was not collected systematically for birds nesting in the different habitat types or at nests with different types of cover but birds nesting in tall bracken (>1.5m) appeared to flush at greater distances (~5-11m compared to 2-7m) than birds nesting in other habitat types. Indeed, nightjars nesting on 4-9 year plantations (where mean vegetation height was >2m) flushed at <3m suggesting that height is less important than the density of cover provided by different vegetation types. This might explain the lower breeding success of bracken nests compared to heathland nests. Adult nightjars are reluctant to flush because it exposes them to predation and discloses the presence of their nest (Samia 2013) or exposes eggs and chicks to desiccation. It was also noted that birds appeared to flush at closer distances (~1-3m compared to 2-6m) at the hottest part of the day on sunny days and this was also recorded for some African nightjar species (Troschianko *et al.* 2016). Stage in the breeding cycle also appeared to affect flushing distance with birds apparently flushing at greater distances to the disturbance when brooding chicks (egg stage mean = 4m, range 2-9, n=14: brooding stage mean = 10m, range 6-15m, n=9). These figures are within the range for incubation but lower for brooding than those recorded by Ruddock and Whitfield (2007). However, they report disturbance distances for nightjars based upon 'safe working distance' disturbance for e.g., forestry work, which are likely to be higher than a controlled disturbance event. The conclusion of this study is that nightjars require a balance between nest crypsis and vigilance negating the need to flush (e.g., Camp *et al.*

2013) and locate nests in intermediate vegetation density and that vegetation type might be an important factor in nest survival.

If nest survival is dependent upon nest crypsis then one would predict that maximum predation should take place early on in the nesting cycle. Selection should act on nest site choice whereby it benefit birds that select nests which minimise predation risk, but also act against suboptimal nest site choice through predation early on in the nesting cycle (Powell and Frasch 2000). Woodfield and Langston (2004) found that all nightjar nests were predated at the egg stage and Murrison (2002) found that 86% of nests failed at the egg stage and this was the finding of this study. When nightjar and artificial nests are combined mean nest survival for bracken clearfells was 10.42 days, mean nest survival for grass clearfell nest was 12.5 days and finally mean nest survival for nests on <4 year plantations was 13.6 day. In contrast, mean nest survival on 4-9 year plantations was 19.2 days and heathland supported a mean survival of 18.4 days. Selection will provide a more immediate measure of predation in the least suitable habitats or nest sites and therefore nest survival is likely to be a good indicator of habitat/nest site suitability and male quality.

It is important to recognise that the experiment was restricted to the incubation period, and not the full breeding cycle, when maximum concealment may be more critical. However, Remes (2005) found that predation of exposed artificial nests was higher than experimentally exposed natural nests of the blackcap concluding that the adult enhances nest crypsis, but this effect was only significant during the incubation period. Predation rates were similar between nightjar and artificial nests in the different habitat categories and at different levels of concealment suggesting that as long as nests are located in optimally dense vegetation there is little requirement for parental defence against visual predators to enhance nest survival. However, nest concealment might be more important when chicks have hatched in reducing the transmission of natural cues such as chick alarm calls. Vegetative concealment of nests increased with time, especially on bracken clearfell

and this is an important mechanism in reducing predation (Burhans and Thompson 1998). This allows us to conclude that the absence of a parent at artificial nests is unlikely to have affected nest survival at the egg stage.

4.4.6 Distance to nearest edge and edge type

Despite the findings of numerous other studies, (Yahner *et al.* 1989, Rudnický and Hunter 1993, ArangoVelez and Kattan 1997, Batary and Baldi 2004), there was no relationship between predation and proximity to edge (Tables 4.5 and 4.6) or nest survival (Table 4.9). A meta-analysis by Vetter (2013) including 9000 nests showed no effect of forest edge on nest predation in tropical species but an effect in temperate species but with significant variability between studies. Woodfield and Langston (2004) found the same effect for nightjar nests in proximity to tracks, roads and forest access points. However, Murison (2002) found that nest success was significantly lower if nests were close to paths or had a higher total length of path within specific distances. Neither study considered the type of edge in terms of abruptness and this might to be important in nest predation (e.g., Lahti 2001).

There was a significant effect of edge type on nest predation and survival wherein nests adjacent to harsh edges experienced more predation (Table 4.5, Figures S4.4 and S4.5), and were predated sooner (Table 4.9, Figures S4.7) than those adjacent to soft edges. In this study 71% of nests occurred adjacent to soft edges and of these 36% (n=35) were depredated, whereas 29% were adjacent to hard edges and 64% (n=26) were depredated. This suggests nightjars are able to gauge the predation threat presented by hard edges, avoiding them because predators focus their hunting along edges and taller vegetation may provide look-out posts for visual predators (Moller 1989, Saracco and Collazo 1999). Both Angelstam (1996) and Lahti (2001) found higher nest predation adjacent to such 'harsh' edges.

4.4.7 Compactness ratio and area

Although there was no significant effect of distance to edge on nest predation or survival, nests in compact territories survived for longer than nests in less compact territories (Table 4.9). This suggests that proximity to edge does affect nest survival but only if that edge is harsh and birds should establish 'rounder' territories where boundaries are harsh. To our knowledge, despite the large number of studies that have considered nest predation in relation to territory size and shape in fragmented habitats, few have looked at territory 'roundness' (for exception see Adams 2001 and Kesler 2012), and thus conclusions regarding its significance are speculative. It appears that it is beneficial to nightjars to defend a compact, rather than an elongated territory because the ratio of perimeter to area is smaller (Grant 1968, Smith 1974, Forman 1985), allowing the territorial male to locate his nest site away from the territory boundary, and thereby reduces the likelihood of predation and extra pair copulations. Birds defended larger territories in the habitats that experienced the highest predation rates (Figure S4.11) and in which nests were predated more rapidly (Table 4.9), suggesting that such habitat cannot sustain denser breeding when the population is larger. We suggest that the defence of large territories in predation-prone locations is a response to the perceived threat of predation (Fontaine and Martin 2006, LaManna *et al.* 2015). The model would not run with 'egg type' as a categorical variable but it would appear that nests containing a quail egg survived longer in more compact territories.

4.4.8 Nest site availability

Although there was no significant effect of number of alternative nest sites on predation rate (Table 4.5), for ground nesting species like the nightjar, suitable nest sites may be scarce. Especially as they require specific substrates, (Cramp 1985, Bowden and Green 1991, Holyoak 2001) as well as sufficient vegetative cover (Woodfield and Langston 2004). Indeed, even marginally suboptimal nest site choice can reduce reproductive success markedly (Martin 1998), so competition for territories containing alternative nest sites should be greatest, (but see Ravenscroft 1989, Bowden and Green 1991). The areas of suitable nesting vegetation in grass and bracken clearfell, and to a lesser extent, <4 year

plantations, were aggregated (clumps of grass/bracken) surrounded by matrices of sparsely vegetated substrate. This may have allowed predators to restrict their search effort to the pockets containing potential prey and hence increase their encounter rate. In contrast, suitable nest patches in 4-9 year plantations and heathland were evenly distributed because of the homogeneity of the habitat. The lack of structural heterogeneity in the vegetation (i.e. the presence of a more continuous cover) in these two habitat categories ameliorates the effects of perceived predation risk, or 'fearscape', making these habitats perceptually more favourable for nesting (Laundré *et al.* 2001, Arias-del Razo *et al.* 2012, Olsoy *et al.* 2015). Not all of the territory was surveyed for alternative nest sites and many will have been overlooked so the number of alternative nest sites might still be an important indicator of territory and male quality.

4.4.9 Benefits of a species specific study

By focusing on a single species and controlling for various factors including: effects of season, lunar synchronicity of egg laying, egg appearance, clutch size, incubation period, nesting density, nest site attributes, proximity to edge habitat, territory attributes, levels of human disturbance and identification of predators, this study was able to calibrate depredation of artificial nests with that of the target species. There were however some aspects of the nesting biology of the target species that we could not replicate - e.g., parental activity at the nest and predation on chicks, and this is a limitation of this study. However, the detailed methodology allows the results to be evaluated and for any methodological artefacts to be distinguishable, allowing for a thorough assessment of internal and external validity (Moore and Robinson, 2004). Methodological and technological improvements for monitoring nests (e.g., Cox *et al.* 2012), or measuring landscape heterogeneity now exist (Olsoy *et al.* 2015). Researchers can combine these with new ecological perspectives and understanding of how predators search (Pelech *et al.* 2010), and the ability to measure the psychological (Clinchy *et al.* 2013) and physiological (Zanette *et al.* 2014) responses of prey to predation threat has led to the development of a more general framework for understanding nest predation. Recent

studies have started to address the warnings and ecologically sensible advice of Major and Kendall (1996) and such developments have allowed researchers to overcome one of the main limitations of using artificial nest experiments as surrogates for real nest predation; internal validity - i.e. differences in predation rates and predators of artificial and real nests. To overcome this, only quail eggs should be used in future experiments as long as they are similar to the target species and miniature cameras at nest can be used to identify predators. However, external validity, the degree to which results can be generalised to other populations or species, remains an issue (Moore and Robinson, Ibáñez-Álamo, Sanllorenzo and Soler 2012, Ibáñez-Álamo *et al.* 2015).

Although rates of nest predation and length of nest survival were similar between nightjar and artificial nests, common predator assemblages did not perpetrate similar levels of predation on nightjar and artificial nests. Plasticine-egg nests attracted more mammalian predation so we conclude that future experiments use 'real' (e.g., quail or chicken) eggs as surrogates for the species under investigation and use camera set-ups to record predation events. Apparently, human visitation of nests had a positive effect on artificial nest survival and nightjar breeding success was similar to previous years so we conclude that controlled visitation of nightjar nests is achievable and future experiments should take measures to control for this important variable. This experiment was able to identify the habitat and ecological variables that led to increased nest success in nightjars and the findings from artificial nests mirrored these so from a conservation perspective it has good external validity. However, caveats proposed nearly two decades ago by Major and Kendall (1996) still need to be borne in mind by researchers who intend to use artificial nest studies as surrogates for predation in wild bird population, and as long as they do, we feel that carefully calibrated artificial nest experiments have an important role in understanding predation in natural populations.

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Appendix

Nest predation

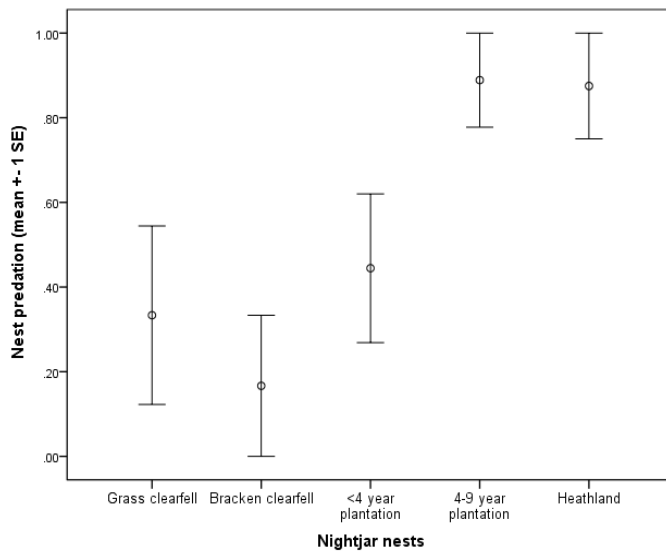


Figure S4.1 Comparison between mean nest predation for nightjars nests in the different habitat categories (± 1 SE). 0 = predated, 1 = unpredated. Therefore a low score is equivalent to higher predation.

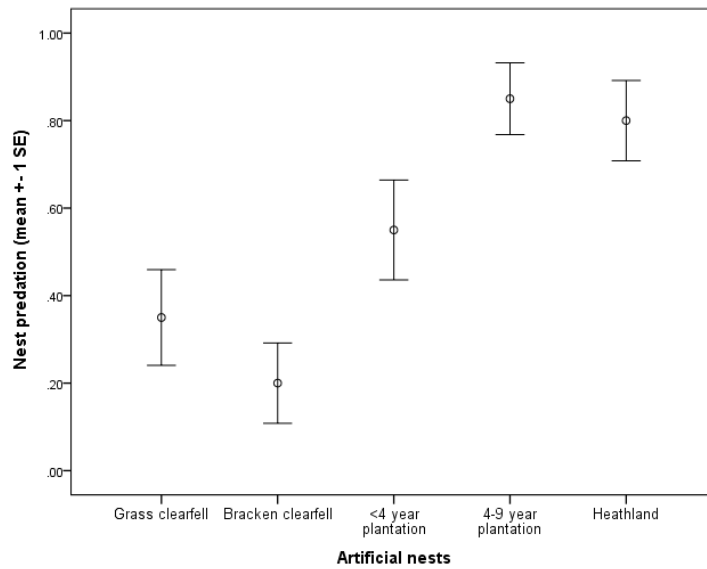


Figure S4.2 Comparison between mean nest predation for artificial nests in the different habitat categories (± 1 SE). 0 = predated, 1 = unpredated. Therefore a low score is equivalent to higher predation.

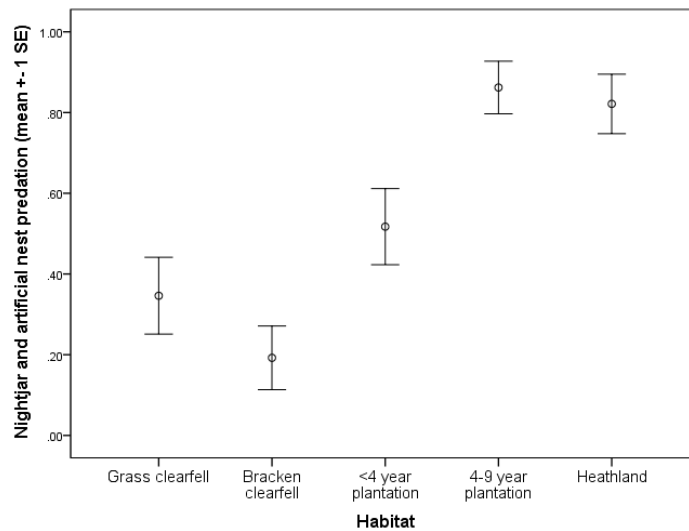


Figure S4.3 Comparison between mean predation rates of pooled nightjar and artificial nests in different habitat categories ($\pm 1SE$). 0 = predated, 1 = unpredated. Therefore a low score is equivalent to higher predation.

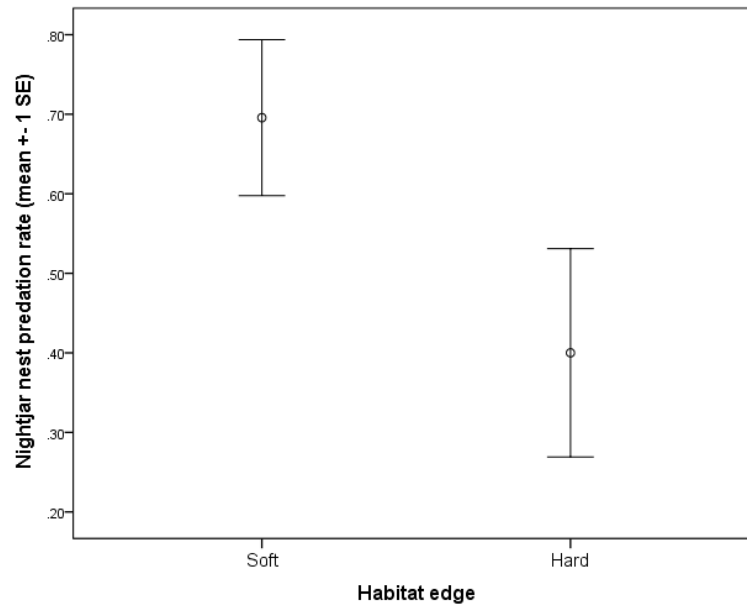


Figure S4.4 Comparison between mean nest predation for nightjar nests adjacent to soft versus hard edges ($\pm 1SE$). 0 = predated, 1 = unpredated. Therefore a low score is equivalent to higher predation.

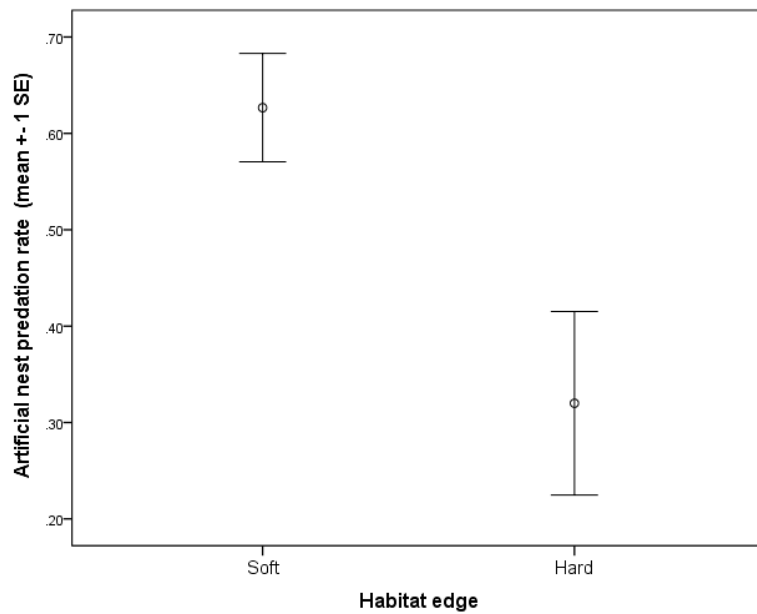


Figure S4.5 Comparison between mean nest predation for artificial nests adjacent to soft versus hard edge ($\pm 1SE$). 0 = predated, 1 = unpredated. Therefore a low score is equivalent to higher predation.

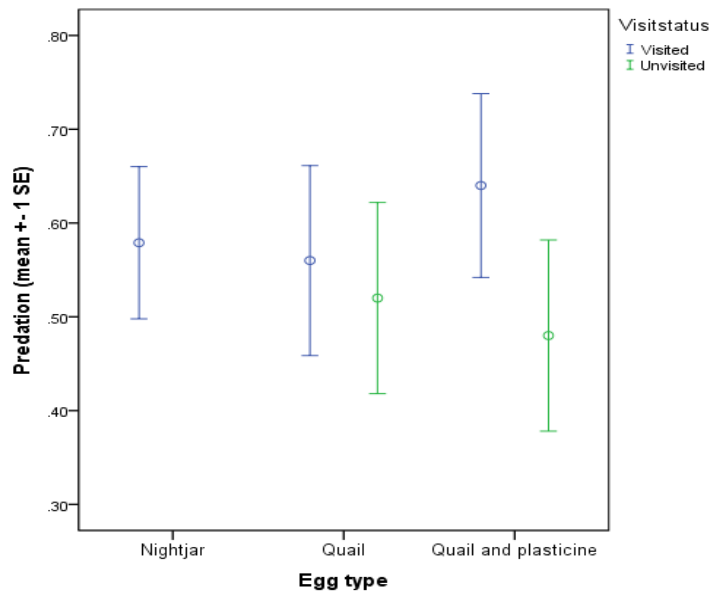


Figure S4.6 Comparison between mean predation rates of nightjar and artificial nests in relation to visit status ($\pm 1SE$). 0 = predated, 1 = unpredated. Therefore a low score is equivalent to higher predation.

Nest Survival

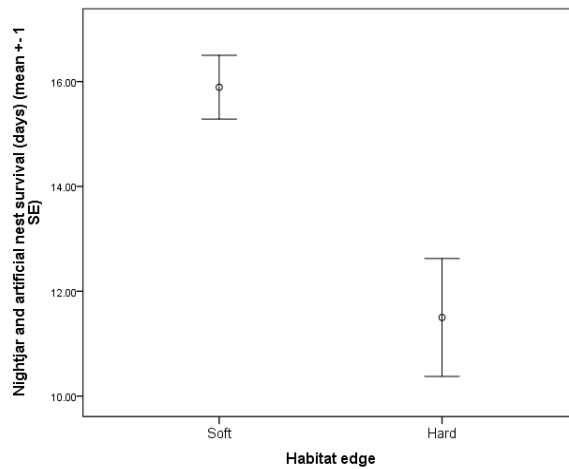


Figure S4.7 Comparison between the mean daily survival ($\pm 1SE$) of pooled nightjar and artificial nests adjacent to soft versus hard edges.

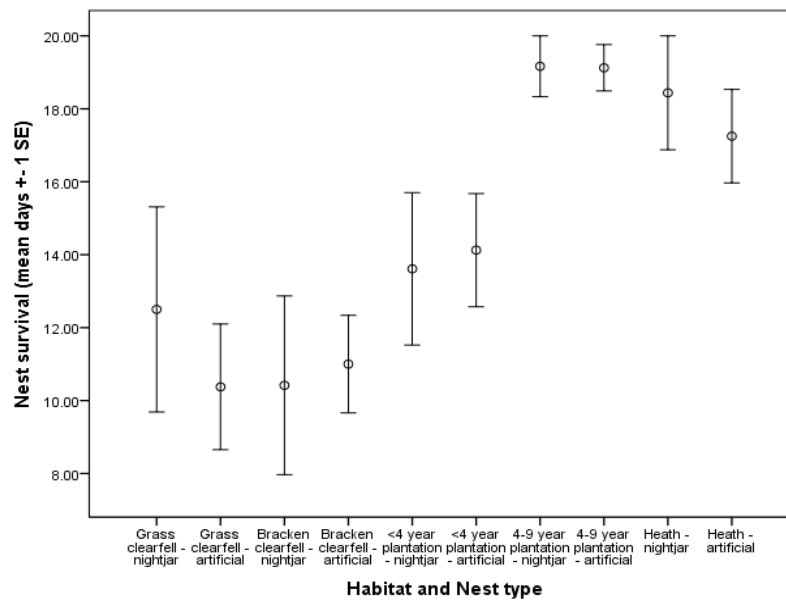


Figure S4.8 Comparison between the mean survival rate (days) of nightjar versus artificial nests within each habitat ($\pm 1SE$).

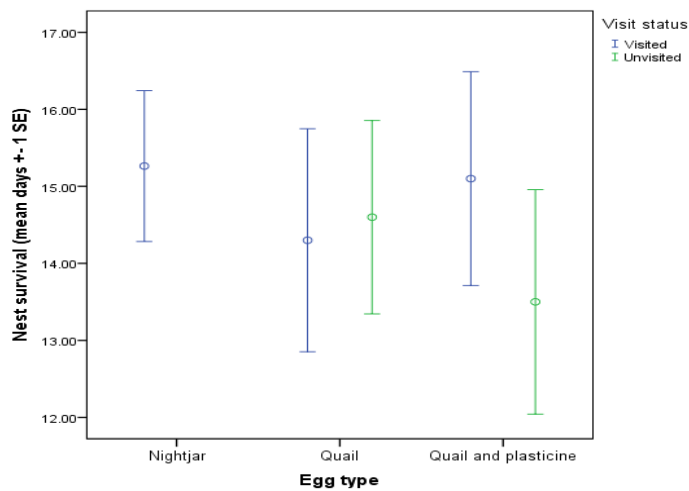


Figure S4.9 Comparison between mean survival rates (days) of nightjar and artificial nests in relation to visit status (\pm 1SE).

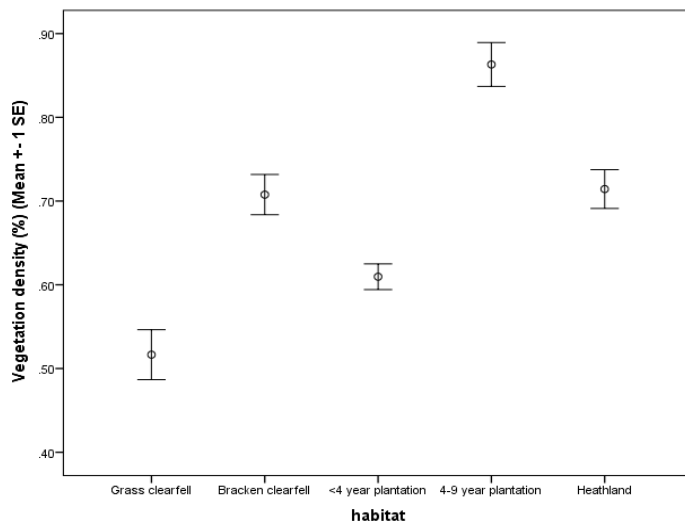


Figure S4.10 Mean vegetation density surrounding nests in different habitats)

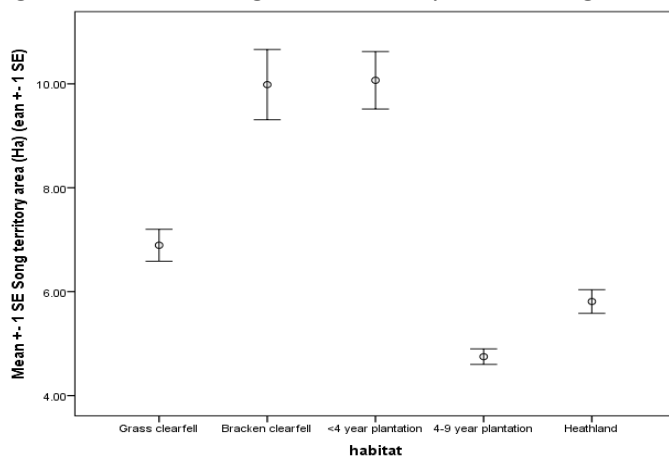


Figure S4.11 Mean area (ha) of song territories in different habitats

CHAPTER FIVE

A MOLECULAR PHYLOGENY OF THE NIGHTJARS (AVES: CAPRIMULGIDAE) SUGGESTS EXTENSIVE CONSERVATION OF PRIMITIVE MORPHOLOGICAL TRAITS ACROSS MULTIPLE LINEAGES

Abstract

We report a molecular reassessment of the classification of the nightjars which draws conclusions that are strongly at odds with the traditional, morphology-based classifications. We used maximum likelihood and Bayesian methods to compare the cytochrome *b* gene for 14 species from seven of the 15 genera of the Caprimulgidae and partial cytochrome *b* sequence data was available for a further seven species including three further genera. We found that within the Caprimulgidae there were four geographically isolated clades with bootstrap support greater than 70%. One of these clades contained just *Chordeiles* species, the remaining three clades each contained a mixture of genera including *Caprimulgus* sp. A clade of exclusively South American nightjars included the genera *Caprimulgus*, *Uropsalis*, *Eleopthreptus* and *Hydropsalis*. A clade of African and Eurasian birds included *Caprimulgus* and *Macrodipteryx*. *Phalaenoptilus nuttallii* and *Caprimulgus vociferous* formed a clade of North American birds. Two ecological factors appear to make morphological classification potentially misleading: first, the apparent retention of primitive anti-predator and foraging-related traits across genetically divergent groups; second, rapid divergence in other traits, especially those related to mating, which generate high levels of morphological divergence between species that are genetically very similar. The cytochrome *b* data suggests that the genus *Caprimulgus* is not monophyletic and is restricted to Africa and Eurasia and that *Caprimulgus* species from outside this area have been misclassified as a consequence of retention of primitive adaptations for crepuscular/nocturnal living. Some other genera also appear to have little support from the cytochrome *b* data.

Keywords: *Eurostopodus*; *Caprimulgus*; Cytochrome *b*; Evolution; Conserved morphology; Primitive traits; MrBayes; Paup; Caprimulgidae; Caprimulgiformes

5.1 INTRODUCTION

The avian nightjar family Caprimulgidae is globally distributed, comprising of eighty-nine species of largely nocturnal insectivorous birds. Molecular classifications by Sibley & Ahlquist (1990) and Mariaux & Braun (1996), confirmed Peters (1940) morphological subdivision of the Caprimulgidae into the Chordeilinae (Nighthawks) that are restricted to the Americas and consist of 10 species, within 4 genera, and the Caprimulginae (Nightjars, Pauraque, Poorwills and Whip-poor-wills) that occur worldwide. Sizes and distribution of genera within the family vary widely, so that whilst the largest and most cosmopolitan genus, *Caprimulgus*, contains 57 species distributed worldwide, all others are geographically restricted, including the smallest such as *Nyctidromus* and *Phalaenoptilus* which are each represented by only a single species.

Nightjar classification and identification are currently phenetic, based predominantly on morphology, song and to a lesser degree behaviour, rather than on molecular characteristics. Typical morphology of Caprimulgidae consists of cryptic and vermiculated plumage, long pointed wings, long tails that vary in form; a small weak bill with a large gape; (Huxley, 1867; Beddard 1886; Hartert, 1897; Glenny, 1953; Hoff, 1966; Buhler, 1970; Cramp, 1985; Sibley and Ahlquist, 1990; Holyoak, 2001). Separation of the Caprimulgidae into the subfamilies Caprimulginae and Chordeilinae is based on palate structure which is schizognathous in Caprimulginae and desmognathous in Chordeilinae (Oberholser, 1914); Caprimulginae also possess conspicuous rictal bristles (although semi-bristles are present in many *Chordeiles*, Bent, 1989). Typical behaviour consists of maintaining crypsis and includes remaining motionless in a prone position when incubating or perched during the daytime; nesting directly on the ground in the majority of species, incubation is typically maternal but with some male involvement especially if double-brooded, (but paternal in *Phalaenoptilus*), most species perform some kind of nest defence and are territorial (Cramp, 1985; Bent, 1989; Cleere, 1999; Holyoak, 2001). At the generic level assignment to genus is based almost exclusively on plumage modifications, song and behaviour (Peters, 1940; Holyoak, 2001), but such differences are increasingly recognised as of

specific rather than generic significance (see recent studies on Pici, Gabulae, and Coracii, Johansson and Ericson, 2003). Most recent studies have been concerned with relationships of families within the order Caprimulgiformes and the relative position of the order to the Strigiformes, Trochilidae and Apodiformes (Mayr, 2002; Fidler *et al.* 2004; Iwaniuk, 2006), and not the reliability of each genus within the family Caprimulgidae. Characteristics have been used to classify Caprimulgidae genera include relative measurements of body size and shape, wing and tarsi length and extent of feathering, plumage characteristics including moult, and are often the records of fieldworkers. Rigorous Hennigian methods have not been used to classify species or genera within the Caprimulgidae and it may be the case that certain plumage characters that have been used to establish new genera have been given excessive weight. Indeed, in the most contemporary review of Nightjar systematics Holyoak (2001) refers to current classification of the genus *Caprimulgus* as a 'rag bag' containing all Caprimulginae lacking any character striking enough to demand treatment as separate genera (Holyoak, 2001. pg 374.). Although *Caprimulgus* may require further subdivision it is also possible that some genera such as *Phalaenoptilus* should be 'merged with *Caprimulgus*' (Holyoak, 2001. pg 343). The generic status of two other genera not sampled in this study, *Podager* and *Nyctidromus* was questioned by Hartert (1897) and by Holyoak (2001) who suggested that they should be suppressed and assigned to *Caprimulgus*. Morphological characteristics associated with vocalisation are also employed to distinguish members of this family e.g., the anatomy of the voice organ and palate (Beddard, 1886); skull bones, (Huxley, 1867); skull and jaw bones (Buhler, 1970); mouth size, (Jackson, 1985); as well as the songs themselves; (Bent, 1989; Cleere, 1998; Holyoak 2001). Indeed, vocalisation has prevailed as one of the primary agents in the 'lumping' and 'splitting' of genera and races (Holyoak 2001; Cleere 1998; Turner *et al.* 1991; Fry 1988; Davis 1962, 1979). In all these cases there is a risk that patterns of variation in morphological or behavioural traits (de Queiroz & Wimberger, 1993) that are mediated by sexual selection and adaptation to habitat gain greater weight in the classifications than characters that are measures of common descent. Furthermore there is such paucity of behavioural information for many genera

within the Caprimulgidae, that a thorough inter-generic comparison of behaviour is not feasible. Hence it is presently unclear whether the relatively widespread distribution of nightjars assigned to the genus *Caprimulgus* is a consequence of worldwide dispersal of a monophyletic genus, a consequence of misclassification due to retained primitive traits across genera or the result of multiple convergence events of distinct genera.

We have constructed phylogeny from the partial sequence of the cytochrome *b* gene of a representative range of Caprimulgid species to test the hypothesis that the genus *Caprimulgus* is monophyletic.

5.2 METHODS

5.2.1 Samples

Blood or tissue samples were collected from live and road kill specimens by licensed bird handlers. Samples were collected from 14 species spread across seven genera. Partial cytochrome *b* sequence data was available for a further seven species including three further genera from Mariaux and Braun (1996) and Espinosa de los Monteros (2000). Sequence data available at Genbank (see Table 1) for representatives Strigidae, Batrachostomidae, Nyctibiidae and Steatornidae, also from Mariaux and Braun (1996) were used as outgroups for phylogenetic analysis.

5.2.2 Whole-genomic DNA Extraction

5.2.2.i Blood, and liver tissues

Samples were stored in DMSO at -20°C , with the exception of tissue from *Nyctidromus albicollis* and blood from *Caprimulgus fossii*, and *C. plumipes*, which were resuspended in Cell Lysis Solution (GenomicPrep Cells and Tissue DNA Isolation Kit, Amersham) and 10 mg/ml of proteinase K solution and then homogenised and incubated overnight at 55°C . DNA was extracted from samples resuspended in Cell Lysis solution DNA using 'GenomicPrep Cells and Tissue DNA Isolation Kit' following the manufacturers' guidelines.

DNA was prepared from samples stored in DMSO by phenol-chloroform extraction followed by ethanol precipitation.

5.2.2.ii Feathers

It was necessary to extract DNA from feathers for only one species, *Macrodipteryx longipennis*, using the silica-gel membrane in QIAquick spin columns (QIAquick™ (QIAGEN®) PCR Purification Kit). Unfortunately, samples available for a further three species: *Caprimulgus donaldsoni*, *C. ruficollis*, and *C. parvulus*; and *Nyctidromus albicollis* did not yield mtDNA of suitable quality for PCR amplification.

The primer used for PCR of light-strand sequence was L14841 (Kocher *et al.* 1989). The heavy-strand primer was H15498 (5'-AAACTGCAGGGAATAAAGTTATCTGGGTCTC-3'; Mariaux and Braun, 1996). PCR products were purified using a QIAquick™ Gel Extraction Kit (QIAGEN®) and sequenced on an ABI373A automated sequencer the PRISM Dye-Deoxy sequencing system (ABI).

Table 5.1 Summary of samples, origins of data and Genbank location codes

Family and scientific name	Sample and source code	Location	GenBank ACCN.	Bases used
Steatornithidae				
<i>Steatornis caripensis</i>	Tissue (a)	Genbank	X95773	101–751
Podargidae				
<i>Podargus papuensis</i>	Tissue (a)	Genbank	X95772	101–751
Batrachostomidae				
<i>Batrachostomus cornutus</i>	Tissue (a)	Genbank	X95776	101–751
Nyctibiidae				
<i>Nyctibius aethereus</i>	Tissue (a)	Genbank	X95781	101–751
Caprimulgidae				
<i>Chordeiles rupestris</i>	Tissue (a)	Genbank	X95778	101–751
<i>Chordeiles acutipennis</i>	Tissue (CW)	N. America	DQ062148	101–751
<i>Chordeiles minor</i>	Tissue (CW)	N. America	DQ062142	101–751
<i>Eurostopodus mystacalis</i>	Tissue (a)	Genbank	X95779	101–751
<i>Eurostopodus papuensis</i>	Tissue (a)	Genbank	X95780	101–751
<i>Phalaenoptilus nuttallii</i>	Blood/tissue (CW)	N. America	DQ062141	101–751
<i>Nyctiphrynus mcleodii</i>	(c)	Genbank	U89195	101–751
<i>Caprimulgus vociferus</i>	(c)	N. America	U89194	101–751
<i>Caprimulgus longirostris</i>	Tissue (b)	S. America	X95777	101–751
<i>Caprimulgus maculicaudus</i>	Blood (RC)	Paraguay	DQ062137	101–751
<i>Caprimulgus e. europaeus</i>	Blood, tissue	UK	DQ062139	101–751
<i>Caprimulgus e. unwini</i>	Blood (DP)	Kenya	DQ062135	101–751
<i>Caprimulgus e. plumipes</i>	Blood (DP)	Kenya	DQ062147	101–751
<i>Caprimulgus fraenetus</i>	Blood, tissue (DP)	Kenya	DQ062136	101–751
<i>Caprimulgus inornatus</i>	Blood (DP)	Kenya	DQ062138	101–751
<i>Caprimulgus climacurus</i>	Blood, tissue (CB)	Gambia	DQ062144	101–751
<i>Caprimulgus candicans</i> ^a	Blood (RC)	Paraguay	DQ062140	101–751
<i>Macrodipteryx longipennis</i>	Tissue, feather (CB)	Gambia	DQ062143	101–751
<i>Hydropsalis brasiliانا</i>	Blood (RC)	Paraguay	DQ062146	101–751
<i>Uropsalis segmentata</i>	(c)	Genbank	AF115898	128–424
<i>Eleothreptus anomalus</i>	Blood (RC)	Paraguay	DQ062145	101–751
Strigidae				
<i>Bubo africanus</i>	Muscle, blood	Genbank	AJ003952	101–751
<i>Bubo bubo</i>	Muscle, blood	Genbank	AJ003965	101–751

Source of sequence data. Taxa with accession numbers in the range DQ062135–DQ062148 were determined in the present study. The bases used column indicates the positions in the complete cytochrome b sequence of *C. vociferus* to which the sequences were aligned. Abbreviations: CB, Clive Barlow; CW, Chris Woods; DP, David Pearson; RC, Rob Clay; PNG, Papua New Guinea. (a) Sequence determined by Mariaux and Braun. (b) Sequence determined by Peter Arctander. (c) Sequence determined by Espinosa de los Monteros. ^a Also termed *Eleothreptus candicans* (Cleere 2002).

DNA sequences were aligned with Clustal. The aligned matrix consisted of 27 taxa (Table 5.1) and 652 nucleotides between bases 101 and 750 in the cytochrome *b* gene of *C. vociferus* GenBank accession number U89194. The bases used relative to *C. vociferus* are shown in Table 1. Bayesian posterior probabilities were computed with MrBayes 3.2.1 (Huelsenbeck and Ronquist, 2001; Ronquist and Huelsenbeck, 2003) by running 1,000,000 MCMC generations using the program default priors on the GTR model. Model parameters were inferred by MrBayes from the data. 1000 trees were sampled from the posterior probability distribution (one every 1000 generations) and 25% were discarded as burn-in to ensure that chains had become stationary.

The most appropriate model for maximum likelihood analysis was identified using hierarchical likelihood ratio tests in Modeltest 3.06 (Posada and Crandall, 1998). Trees were identified using a heuristic search with maximum likelihood in PAUP 4.10b (Swofford, 1998) with the model and parameters identified in Modeltest. One hundred bootstrap replicates were also evaluated using a heuristic search in PAUP. The constancy of the rate of substitution in different branches of the tree was tested using the likelihood ratio test (Felsenstein, 1981). Alternative tree topologies were evaluated by the method of Shimodaira and Hasegawa (1999) implemented in PAUP.

5.3 RESULTS

5.3.1 Monophyly of the Caprimulgidae.

Trees of 21 caprimulgid taxa were compiled using Bayesian and maximum likelihood (ML) using a single member of each of the following Caprimulgiformes genera *Steatornis*, *Podargus*, *Nyctibius*, and *Batrachostomus* to root the Caprimulgidae, the complete tree was rooted on two species of *Bubo* (Fig. 1).

Seven of the 14 genera recognised by Cleere (1998) in the Caprimulgidae were represented in these classifications. These genera clustered in a single clade although it had no statistical support in either Bayesian or ML trees. The genus *Eurostopodus* is

included in the family Caprimulgidae by Holyoak (2001) but not by Cleere (1998), *Eurostopodus* was external to the Caprimulgidae in the best Bayesian and ML trees although since the Bayesian and ML support for the relevant nodes was low the classification of this genus cannot be inferred from this data. The inclusion of *Eurostopodus* in a clade containing the other Caprimulgidae genera was not rejected by the Shimodaira and Hasegawa test. Therefore, although the definition of Caprimulgidae of Holyoak (2001) that included *Eurostopodus* cannot be excluded, the definition used by Cleere (1998) that did not include *Eurostopodus* will be used here.

5.3.2 Monophyly of Genera within the Caprimulgidae and geographical clustering

Within the Caprimulgidae there were three clades with posterior probabilities greater than 0.99 (Fig. 1). The same clades were seen in the ML tree with bootstrap support greater than 92%. Additionally, a Nearctic clade containing *Phaenoptilus nuttallii* and *Caprimulgus vociferus* had weak bootstrap support (72%) and a Bayesian posterior probability of (0.94). *Nyctiphrynus mcleodii* did not cluster with any other Caprimulgidae included here. One clade contained just *Chordeiles* species and appeared monophyletic. The well supported Neotropical and African clades each contained a mixture of genera including *Caprimulgus*. Although the clades of Caprimulgidae contained a mixture of taxa there was strong geographic clustering. One weakly supported North American clade contained *Caprimulgus vociferus* and *Phaenoptilus nuttallii* and another just *Chordeiles* spp.; a South American clade contained three *Caprimulgus* species, and *Eleothreptus anomalus*, *Hydropsalis brasiliensis* and *Uropsalis segmentata*; and an African clade contained *Macrodipteryx longipennis*, *Caprimulgus europaeus*, (which migrates to the western Palearctic to breed), and three other *Caprimulgus* species which are permanent residents of Africa. The hypothesis that species within the genus *Caprimulgus* as currently described are a monophyletic clade was compared with the alternative hypothesis represented by the tree presented in Fig. 5.1 using the Shimodaira–Hasegawa test. This test rejected the hypothesis that the genus *Caprimulgus* is monophyletic ($p < 0.05$).

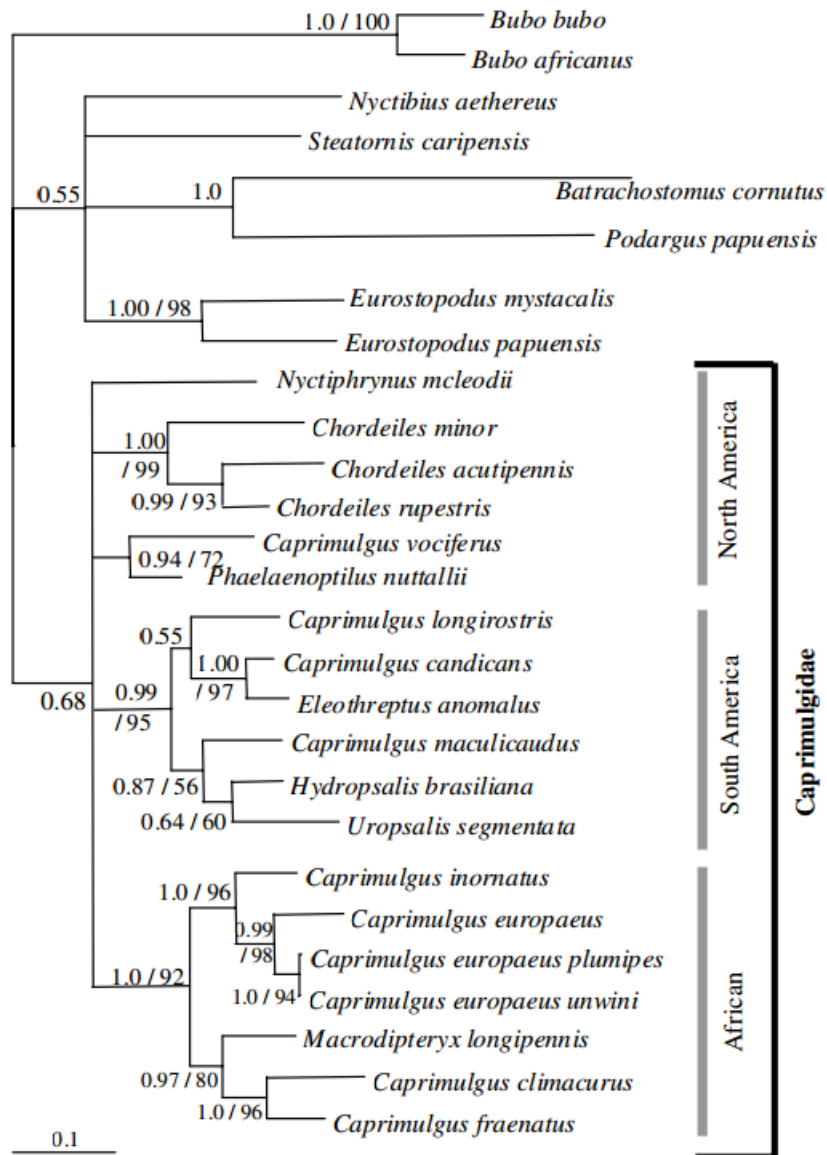


Fig. 5.1 Bayesian tree of Caprimulgiformes, rooted on the Strigidae, compiled with Mr. Bayes. A ML tree had identical topology for supported nodes. Bootstrap values from the ML tree are shown after the Bayesian posterior probabilities where they were greater than 50. The ML tree was compiled with PaupV4.10b using the General Time Reversible Model with gamma distribution of variability of sites. GC composition was 50% but other parameters were highly skewed, relative transition and transversion rates were: A \leftrightarrow C 0.85; A \leftrightarrow G 9.54; A \leftrightarrow T 2.17; C \leftrightarrow G 0.41; C \leftrightarrow T 11.90; G \leftrightarrow T 1.00; proportion of invariable sites 0; gamma distribution rate parameter 0.257.

A parsimony tree was also compiled which contained the same four major clades of Caprimulgidae as the ML tree (not shown). Bootstrap values were generally lower and

there were two differences in topology within the major clades between the parsimony and ML trees that are described in the appropriate sections below.

5.3.3 Evolutionary Rates and relationships among clades

None of the methods could determine the relationship between any of the four Caprimulgidae clades with confidence. A series of likelihood ratio test was applied by systematically removing clades or species within the Caprimulgidae to identify the largest set of Caprimulgidae taxa for which the likelihood ratio test did not reject the molecular clock. The molecular clock hypothesis could not be rejected for the Caprimulgidae if just *P. nuttallii* was excluded ($p < 0.52$) or if just *C. europaeus* was excluded ($p = 0.16$). Since both *P. nuttallii* and *C. europaeus* could individually cause the data to appear non-clock-like the effect of excluding both these taxa on bootstrap values was tested. However, despite the exclusion of these taxa, bootstrap values for relationships between the major geographical groups were still less than 50% and therefore, it seems unlikely that the difficulty in resolving relationships between major clades of Caprimulgidae is due to rate variation. It is possible that the difficulty in resolving relationships within the Caprimulgidae is due to a combination of a rapid radiation event followed by saturation of the relatively rapidly evolving cytochrome *b* gene over the long periods of time that this group appears to have existed (Cibois *et al.* 1999; DeFilippis and Moore, 2000). The mean transition/transversion ratio between taxa within each of the four clades within the Caprimulgidae was 5.0 whilst the mean ratio between taxa in different Caprimulgidae clades was 2.3, this being indicative of some degree of saturation. A phylogeny of a less rapidly evolving gene nuclear may help to resolve these relationships (Hughes, 1999; Sheldon *et al.* 2000), but a radiation event may be impossible to resolve. The Caprimulgidae appear to be an exception to the observations of Moore and DeFilippis (1997) who concluded that the utility of cytochrome *b* is most effective at resolving avian diversification at the level of families through to sub-species.

5.4 DISCUSSION

The most striking feature of the cytochrome *b* classification is the clustering based on geography rather than existing nomenclature. Incongruences between geographical clades based on molecular phylogenetic hypotheses and those derived from morphology have been demonstrated in a diverse range of organisms including Asian wood-feeding cockroaches (Maekawa *et al.* 1999), fire salamanders (García-París *et al.* 2003) and tragopans (Randi *et al.* 2000). Such geographical clustering suggests that many *Caprimulgus* species have been misclassified as a consequence of excessive weight being attached to some morphological characters; for example the exaggerated secondary sexual features of *Macrodipteryx* and *Uropsalis* and the consequent creation of distinct genera for birds that have very similar cytochrome *b* genes. Convergent evolution has confounded classifications of birds in some cases, for example, the Gymnogene (*Polyboroides typus*) and the Crane Hawk (*Geranospiza caerulescens*), from South America and Southern Africa were believed to be closely related based on shared morphology and a remarkably mobile intertarsal joint, but mitochondrial and nuclear DNA sequences have shown these features to be convergent adaptations for extracting prey from rock crevices (Lerner and Mindell, 2005). The Caprimulgidae form the most striking example of conserved primitive traits within birds, of which we are aware, that has confounded the morphology based classification. This is particularly the case in South America where there are four caprimulgid genera (*Caprimulgus*, *Hydropsalis*, *Uropsalis* and *Eleothreptus*) that have less genetic diversity between them (maximum Jukes Cantor distance 0.112) than found within the *Caprimulgus* species of the Old World (maximum distance 0.131). Indeed, *Hydropsalis brasiliانا* and *Uropsalis segmentata* are no more genetically divergent (Jukes Cantor distance 0.079) than the subspecies *Caprimulgus. e. europaeus* and *C. e. plumipes* (0.081). Hence, Caprimulgidae present a remarkable case study in which key components of morphology that have been used for classification turn out to be unreliable phylogenetic markers. *Hydropsalis* spp. differ from *Caprimulgus* in having trident shaped tails that are especially evident in the males, and *Uropsalis* spp. males have extremely elongated outer tail feathers (Cleere 1998). Otherwise, these genera are similar

in habit and appearance to other Neotropical *Caprimulgus* spp. It would appear that species from Africa and South and North America have been included in the genus *Caprimulgus* because primitive traits (morphology, cryptic plumage and behaviour) have been retained because the lifestyle of crepuscular/nocturnal hunting on the wing with diurnal ground nesting has been retained. In contrast, local adaptation and sexual selection may have led to morphological/behavioural changes that have appeared to be sufficiently large in the context of the general uniformity of *Caprimulgus* to warrant genus status for *Hydropsalis* and *Uropsalis* when compared with *Caprimulgus*. The minor differences in the cytochrome *b* gene associated with these morphological changes suggest that the underlying genetic differences between *Hydropsalis* and *Uropsalis*, on the one hand, and *Caprimulgus*, on the other, are small. The *Eleothreptus anomalus* and *Caprimulgus candicans* clade had high (99%) bootstrap support and a high posterior probability (1.00). This is consistent with observations of similarity made in the Weld (Cleere 1998; Cleere, 2002; Clay, personal communication). Indeed, Cleere (2002) has assigned *C. candicans* to the genus *Eleothreptus* on the basis of morphological, vocal and behavioural similarities. Similarities include plumage detail, outer primaries that are slightly bent inwards, a short tail, broad bill with particularly long rictal bristles and partially feathered tarsi. Both species use mechanical wing sounds, which are thought to emanate from the modified outer primaries, during courtship display. Some of these features occur widely in Neotropical *Caprimulgus* and could simply be convergent adaptations or indeed primitive traits. *Eleothreptus anomalus* and *Caprimulgus candicans* are considered allopatric, possibly parapatric in places. There is paucity in distribution data but both breed in grasslands with scattered trees (Cleere 1998). *Eleothreptus anomalus* shows a preference for grassland near to wet areas (Lowen, personal communication). *C. longirostris* is reported as being more similar to *C. candicans* than other *Caprimulgus* sp. in possessing a square tail, stout rictal bristles, extensive white in outer primaries and retrices, rounded wings, and also size, (Holyoak, 2001) and this was supported by the ML and Bayesian trees but not the parsimony one.

Within the African clade *Macrodipteryx longipennis* clustered with *C. fraenatus* and *C. climacurus* in the ML and Bayesian trees although with weak support. In a parsimony tree *Macrodipteryx longipennis* was external to all other African *Caprimulgus*, although with only weak bootstrap support (65%). There are two species of *Macrodipteryx*; *M. vexillarius* (not included here) and *M. longipennis*. They are distinguished from *Caprimulgus* by extremely elongated second primaries P2, which are displayed during courtship, a short cranium and very short, triangular bill (Holyoak, 2001). *Macrodipteryx* spp. are two of the few nightjars that are known to be polygynous and this may account for the exaggerated plumage of these two species. *Macrodipteryx* is also a lek breeder and, as with other lek species, such as *Uropsalis*, there may have been rapid evolution of display plumes due to extreme sexual selection leading to such sexual dimorphism and dichromatism (Hoglund, 1989; Oakes, 1992). Therefore, it is possible that *Macrodipteryx* is a relatively recent descendant of a *Caprimulgus* ancestor. The only other member of the genus, *Macrodipteryx vexillarius*, is considered a close relative of *M. longipennis* but is considerably heavier, possessing a flatter-skull, and differing in the form of feather P2, development of PP3-7, and amount of white in plumage (Holyoak, 2001; Fry, 1988).

The Nearctic clade containing *Phalaenoptilus nuttallii* and *Caprimulgus vociferous* has 72% ML bootstrap support (Fig. 5.1). *Phalaenoptilus nuttallii* is a monotypic genus and is morphologically similar to *Caprimulgus*, the genus to which *P. nuttallii* was originally ascribed when first described by Audubon (1844). *Phalaenoptilus nuttallii* may have diverged from *Caprimulgus* relatively recently which is consistent with the sequence of divergence proposed by Sibley and Ahlquist (1990). Morphological similarities of *Caprimulgus* to *Phalaenoptilus* include a proportionately large head, soft plumage, slightly rounded tail and the length of the uppertail coverts (Bent, 1989). A tenuous morphological dissimilarity is that the tarsi in *Phalaenoptilus* are unfeathered, although tarsal feathering varies considerably in the Old World true nightjars (Holyoak, 2001).

There was clear evidence of saturation in the cytochrome *b* sequence data, suggesting that the nightjar family might be relatively ancient compared to other bird families since the cytochrome *b* is generally useful for resolving relationships within avian families (Moore and DeFilippis, 1997). If this is the case, then a more slowly evolving marker may help resolve the relationships of major clades within this family. However, it is also possible that the geographical clades radiated over a relatively short period of time making it difficult to resolve the relationships between them by any method.

The polyphyly of the genera of the family Caprimulgidae provides evidence that this is a particularly difficult family to classify on morphological grounds. This may be attributed to the constraints imposed by night-time aerial feeding. Primarily, the requirement for camouflage to avoid detection by diurnal predators results in the cryptic plumage characteristic of all Caprimulgiformes, and also of the related crepuscular order the Strigiformes. The crepuscular/ nocturnal feeding niche is divided between aerial feeders, such as the Caprimulgidae and those other Caprimulgiformes that feed in the air and on the ground, namely the Potoos (Nyctibiidae), Frogmouths (Podargidae) and the Owlet-nightjars (Aegothelidae) that are largely terrestrial feeders. Morphological characteristics of the nightjars are their cryptic plumage, large eyes and gape, weak bills, rictal bristles (reduced in Chordeilinae), long tail and wings, and low wing loads. The polyphyly of the family Caprimulgidae suggests that these characteristics are primitive traits that have been retained in the African, North American and South American clades. The alternative hypothesis, that these common characteristics are a consequence of convergent evolution on a morphology adapted for aerial feeding and cryptic plumage for diurnal ground nesting, cannot be excluded, but is less parsimonious since it would require at least two separate convergences on the same morphology.

5.4.1 Evolution

Although insufficient fossil data is available to calibrate the phylogeny of the Caprimulgidae for the time scales which are resolved in the trees presented here, the

trees do have some implications for the evolution of the family Caprimulgidae. The DNA–DNA hybridisation data for the divergence of Strigiformes and Caprimulgiformes of 44.9 MYA and the Caprimulgidae at 39.7 MYA renders an early date for the radiation of the family associated with Continental break-up improbable (Sibley and Ahlquist, 1990). *Ventivorus ragei* is the earliest fossil Caprimulgidae and has been dated to the Eocene about 40 MYA in France ((2)), which provides little support for a very early origin of the family and supports the DNA–DNA hybridisation hypothesis. However, the earliest Caprimulgiform fossil, *Prefica nivea* dates from the Lower Eocene (50.5–54.9 MYA), suggesting that the DNA–DNA hybridisation dates for divergence are too low. It is possible, therefore, that the Caprimulgidae radiated in the Eocene and that descendants of that radiation evolved independently on the separate continents but retained many features of the primitive morphology.

Caprimulgus europaeus, *Caprimulgus ruficollis*, *Caprimulgus aegypticus* and *Caprimulgus nubicus* are the only species of *Caprimulgus* that breed in the Western Palaearctic and all migrate from Africa each spring. There are 20 Afrotropical species of *Caprimulgus* (Cleere and Nurney, 1998). The current migrations of *Caprimulgus europaeus* subspecies can only have developed since the end of the last ice age, presumably from birds resident in Africa or southern European refugia. This is supported by the ‘Southern ancestral home theories’, demonstrated for many other avian species including Chaffinch (*Fringilla coelebs*) (Griswold and Baker, 2002), Blackcap *Sylvia atricapilla* (Pérez-Tris *et al.* 2004) and Great Tit, *Parus major*, (Kvist *et al.* 1999), that colonised seasonally suitable habitat from southern refugia during glacial retreat. The maximum likelihood and parsimony trees show that the closest relatives of *Caprimulgus europaeus* are African suggesting that *Caprimulgus europaeus* evolved from an African species. Indeed, Fry (1988) concluded the *C. europaeus* is closely related to *C. rufigena* (not included in this study) that is a resident breeder in South Africa. The alternative hypothesis, that *Caprimulgus europaeus* was indigenous to Europe and Asia and acquired a migratory habit to Africa to adapt to the

cooling climate, cannot be excluded until a calibrated tree is available. The addition of Asian species of *Caprimulgus* to the tree may help resolve the origin of *C. europaeus*.

5.4.2 Conclusion

Fossil Caprimulgidae are known from the Eocene (Holyoak, 2001; Cleere 1998; Mourer-Chauvire, 1988). They have radiated into a diverse range of habitats and colonised all the continents except Antarctica. If the modern birds are descendants of that original radiation, their highly conserved morphology is even more remarkable, and demonstrates the extreme physiological constraints imposed by adaptation to crepuscular/nocturnal living combined with ground nesting. It would seem that such constraints are so severe that morphological similarities are genuinely homologous; the alternative explanation of strongly convergent evolution is in our view less parsimonious, requiring the independent evolution of extensive morphological similarity in phylogeographically distinct groups.

Of equal importance, analysis of cytochrome *b* sequence data provides evidence for rapid morphological evolution of certain behaviours and secondary sexual characteristics. For example, unlike *Caprimulgus*, *Macrodipteryx* and *Uropsalis* are polygynous. Members of these latter genera are distinguished by exaggerated tail and wing feathers used in courtship displays. We suggest that such changes in mating system may have driven rapid morphological change that appears significant in relation to the similarity between the 57 species of *Caprimulgus* but may not be good markers for significant genetic divergence. Consequently, the nightjars appear to contain examples of morphologies and behaviours that remain stable over tens of millions of years, as well as examples of rapid morphological changes in response to changing behaviours.

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CHAPTER SIX

RICTAL BRISTLES IN THE CAPRIMULGIFORMES ARE SPECIALISED FOR MECHANORECEPTION AND PROTECTION DURING FORAGING IN COMPLEX HABITATS

Abstract

Foraging methods and diet choice are major components defining an animal's niche. Within an ecological context, the divergence of foraging methods across environmental gradients may promote or reinforce local adaptation of behavioural, morphological and physiological traits and may ultimately lead to reproductive divergence and speciation. We present a phylogenetically-controlled comparative analysis of bristle characteristics in the Caprimulgiformes (nightjars, nighthawks, and relatives). Facial and head bristles were sampled from museum specimens. Interspecific variation in rictal bristle number, length and stiffness is high in the nightjars, with functional bristles absent in the majority of the nighthawks (Chordeilinae) and considerable variation in the remaining two New World nightjar radiations and the Old World radiation. Our analyses showed that rictal bristle number and characteristics correlated with foraging habitat complexity, mouth area and foraging method, but less so with general habitat complexity. Based on our results we suggest that rictal bristle number has a mechanical role in protecting delicate head structures from obstacles in general and foraging habitats. We also propose that complex foraging habitats select for longer, more flexible rictal bristles that have improved mechanoreception. It would appear from our results that nesting ecology has little effect on the presence of different bristles. Bristles are primitive and have become vestigial multiple times within this Order. These events are associated with habitat shifts leading to changes in foraging behaviour and selection on bristle characteristics, which in turn may have led to speciation in these successful and enigmatic nocturnal birds.

Keywords: rictal bristles, nightjars, foraging behaviour, form and function, niche differentiation, habitat specialisation, general habitat, comparative method, speciation

6.1 INTRODUCTION

Variation in key ecological variables across habitats promotes and reinforces local adaptation in behavioural, morphological and physiological traits, and may ultimately lead to reproductive divergence and speciation. Phylogenetically controlled examinations of such ecological correlates have been widely used to explain function and variation in a range of traits from the eye colour of mantellids (Amat *et al.* 2013), to range expansion in *Lepidoptera* (Matilla *et al.* 2011). Examining ecological correlates in this way may be particularly useful for understanding the evolution of foraging behaviour and feeding structures, since foraging habitats can be well defined. Examples include small intestine length and feeding habits in birds (Lavin *et al.* 2008), and the morphology of hands and feet of callitrichid primates in relation to foraging ecology (Smith and Smith 2013).

Bristles - modified stiffened feathers - on the face and head are widespread among birds and members of at least 78 bird families possess them (del Hoyo, 2014). Bristles range from branched semi-bristles to the barbless rictal bristle (Figure 1). Facial bristles typically occur at the rictus (corner of the mouth), lores (between mouth and eye), nares (nostrils), basal (base of bill), interramus (under the lower mandible), malar (cheek, below eye), and the forehead, including eyelashes. Rictal bristles are specialised, usually barbless feathers with numerous sensory receptors (Kuster 1905, Lucas and Stettenheim 1972, Stettenheim 1973, 2000, Cunningham, Alley and Castro 2011). They are characterised by a reduction or absence of barbs and barbules. They have a tapered rachis, with a concentration of melanin, especially towards the tip (Bonser 1996). The reduction in barb number and barbule structure originates in the follicle and is not due to abrasion during life (Brush 2000, Prum and Brush 2002).

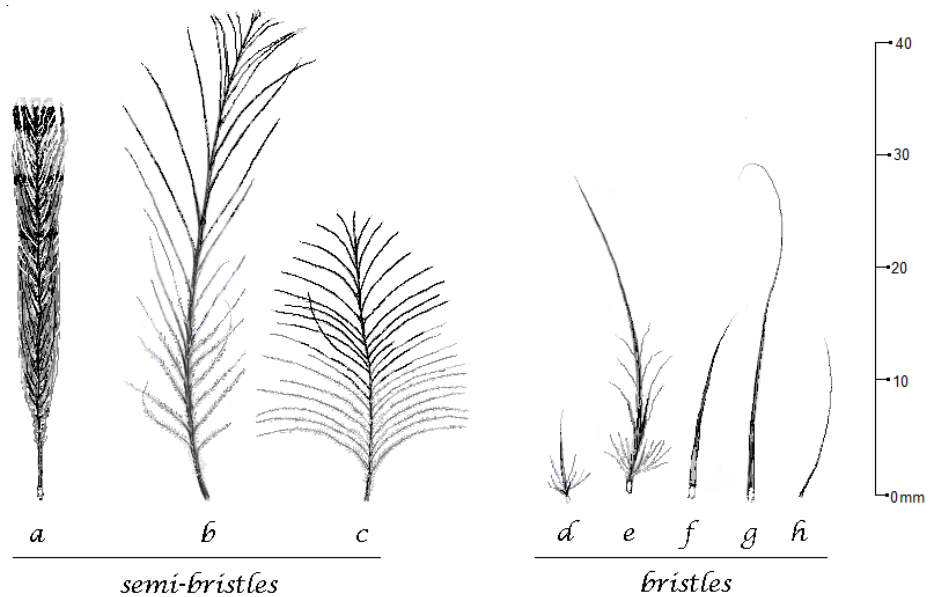


Figure 6.1 Sketches of museum specimens showing examples of semi-bristles and bristles. Semi-bristles are branched with a stiff rachis (shaft) and may be (A) feather-like with a high concentration of barbules especially towards the tip of barbs (specific to the region at the base of the upper mandible and between the eyes of larger frogmouth species); (B) less densely barbed (head and face in frogmouths and owl-nightjars), or (C) a shorter less stiff rachis with barbules along the base of the rachis and the lower barbs (between the eyes and on the nares in potoos). Bristles also take various forms but the most frequent types consist of (D) a short rachis with barbs at the base (basal region of most large Caprimulgiformes); (E) a long rachis with barbs at the base and extending up the rachis (interramus region and lores on frogmouths, potoos and oilbird); (F, G) a medium or long rachis normally devoid of barbs (rictus of most true-nightjars), (H) thin and hair like taking the form of eye lashes (surrounding the eyes of potoos and frogmouths).

The function of bristles remains unclear (Cunningham *et al.* 2011). There is some evidence of selection for bristles in species that are nocturnal and crepuscular, nest in enclosed spaces, and have a range of feeding habits including aerial insectivory, wood boring and ground feeding. However, not all genera within families and not all members of each species possess bristles and they are absent from many species with similar life histories to those species that possess them. Further behavioural or comparative studies, involving a well-supported phylogenetically controlled methodology are therefore required to determine the function and evolution of these specialised feathers in the bird families in which they occur.

6.1.1 Hypotheses About Bristle Function

Four broad functions have been proposed for bristles.

(i) Rictal bristles are sometimes considered adaptations for head protection from prey (Dyer 1976) and hard surfaces such as foliage when feeding on the wing (Brush 1967, Conover and Miller 1980, Martin 1990). In support of this, Leisler and Winkler (1985) noted longer rictal bristles in aerial foraging birds and Keast and Sanders (1991) found that more volant species of kinglets (*Regulus calendula* and *R. satrapa*) possessed longer rictal bristles than arboreal feeders. In both cases, protection from insects caught in flight seems plausible. Dyer (1976) argued that they serve to protect the eyes from the legs and stings of potentially hazardous prey such as bees and grasshoppers. Protection from vegetation might be equally important. Members of the *Thamnophilidae* forage by darting into foliage, which typically involves forceful contact between the head and the vegetation; the concentration of stiff bristles may serve to protect the eyes (del Hoyo 2015).

(ii) A putative function for rictal bristles, as ‘insect-catching nets’ funnelling prey into the mouth (Welty 1962, Van Tyne and Berger 1965), seems to have been disproved for certain species (Dyer 1976, Conover and Miller 1980). In a controlled experiment performed on Willow flycatchers (*Empidonax traillii*) Conover and Miller (1980) showed that rictal bristles protect the eyes but do not aid in capture of prey and this was also supported by observational work by Lederer (1972) and Dyer (1976). Leisler and Thaler (1982) found that Firecrest (*Regulus ignicapilla*) possess longer rictal bristles than the conspecific Goldcrest (*R. regulus*) allowing them to capture larger prey by trapping it beneath the bristles. Cunningham *et al.* (2011) suggest that rictal bristles might provide tactile information about prey when it is captured and that other facial bristles might provide information on air flow, allowing aerial insectivores to precisely locate prey at close quarters. Jackson (2007) proposes that the structure and position of rictal bristles in nightjars suggests a dual role for eye protection and insect capture. He argues that the

position of bristles along the tomium in front of the eye means that they allow the bird to see but would 'bounce' flying legs or wings away from the eyes and into the mouth. He suggests that because the bristles provide resistance when pushed towards the eye, but not in the opposite direction, supports a dual function.

(iii) Stiff facial bristles are present in some species of raptor and carrion eater and these may prevent contamination of the plumage while the bird is feeding (Chandler 1914).

(iv) Rictal and other head bristles may have a broader mechanosensory function (Lucas and Stettenheim 1972, Stettenheim 1972, Seneviratne & Jones 2008, 2010), giving information about the animal's immediate environment. Cunningham *et al.* (2011) found high concentrations of sensory receptors (Herbst corpuscles) at the base of bristles in the nocturnal and hole nesting brown kiwi (*Apteryx mantelli*), morepork (*Ninox novaezealandae*), and Hihi (*Notiomystis cincta*), suggesting a mechanosensory role in these species.

Other functions for bristles have been proposed in other avian species. *Bucerotidae* possess long eyelashes which act as sunshades (Martin and Coetze, 2004). Jany (1955) suggested that rictal bristles on the upper mandible may even act as contact chemoreceptors but this has not been substantiated. There are no apparent structures within the keratin of bristles that allows them to detect chemical molecules so it is unlikely they are involved in olfaction or gustation.

6.1.2 Caprimulgiformes: A Case Study

Here we focus on the avian Order Caprimulgiformes, comprising of 135 globally distributed species (Holyoak 2001) of predominantly nocturnal insectivorous birds that occupy a diverse range of habitats, including desert, rocky outcrops, savannah, scrub and dense tropical forests. Caprimulgiformes breed from sea-level to 4,200 meters above sea

level and from Finland (N 60°) to Tierra del Fuego (S 60°) (Cleere 1998, 1999, Holyoak 2001). Relationships among species are well resolved and members of the five Caprimulgiform families included in this study (Figure 6.2) possess facial bristles. There is a diverse range of feeding and breeding ecologies (Appendix A, Table 3), and significant variation in bristle number and characters. Bristles are primitive within this group and are either absent or range from short, stiff, barbless rictal bristles (Figure 6.3A), long, semi-stiff, barbless rictal bristles (Figure 6.3B) to long, flexible, barbed semi-bristles (Figure 6.3C).

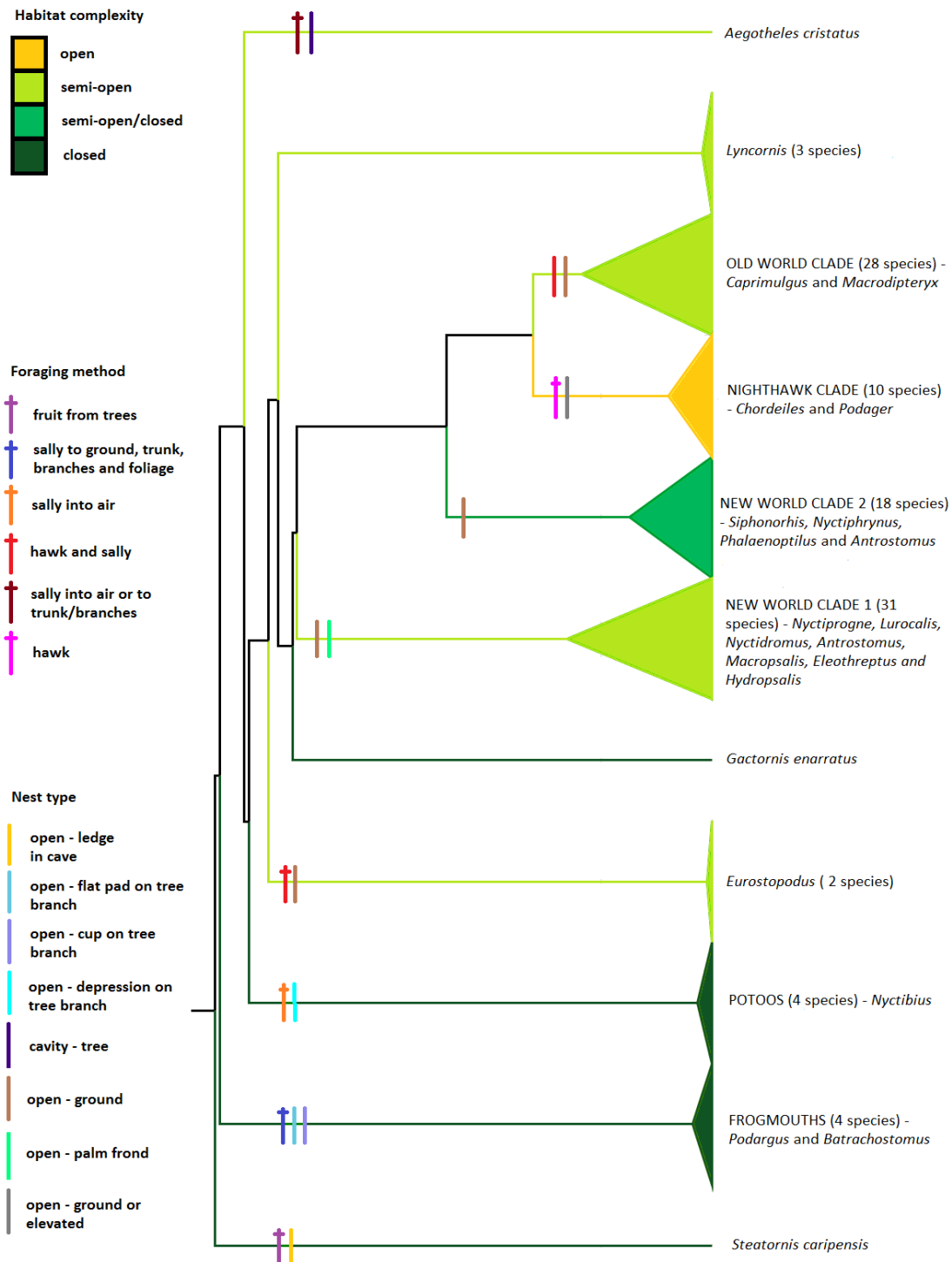


Figure 6.2 Phylogenetic overview of relationships among the main clades of the Caprimulgiformes. Numbers in brackets represent the number of species and races sampled in this study. The coloured triangles represent the mean habitat scores for all the species in the clade and is scored as: ≤ 1.5 'open', $>1.5 \leq 3$ 'semi-open', $>3 \leq 4.5$ 'semi-open/closed' and >4.5 'closed'. Foraging method and nest type are displayed in branches as coloured crosses and bars respectively.



(A)

(B)

(C)

Figure 6.3 Examples of bristles on (A) *Antrostomus parvulus*, (B) *Nyctiphrynus mcleodii* and (C) *Batrachostomus javensis*. *A. parvulus* has rictal bristles (Figure 6.1 - f) extending forward and downward from the rictus and tomium (edge of bill) with a slight upward curve. Similarly, *N. mcleodii* has rictal bristles (Figure 6.1 - g) extending forward and downward but with a downward curve and bristles above the eye (Figure 6.1 - h). *B. javensis* has rictal bristles (Figure 6.1 - e, g) with a downward projection and curve and bristles at the interramus, basal region (Figure 6.1 - d, e), surrounding the eye (Figure 6.1 - h) and semi-bristles on the forehead and between the eyes (Figure 6.1 - b, c), crown, ear covert and nape (Figure 6.1 - b). Credit: A - Phil Palmer, www.BirdHolidays.co.uk; B - Pete Morris, www.Birdquest.com; C - James Eaton, www.BirdtourAsia.co.uk

We predicted that bristle characteristics in Caprimulgiformes would be determined by their ecological function and therefore arrived at the following hypotheses:

- a. If rictal bristles were required for prey capture (including detection and manipulation) we expect all aerial feeding species to possess them. We expect them to be thick (short and stiff) and barbed to aid in prey capture.
- b. If rictal bristles were for mechanical protection from prey we expect all species to possess them. If they provide protection from vegetation we expect species that sally, or hawk and sally, and forage amongst vegetation, and ground feeding species to possess them but not those species that hawk high above the ground. We also expect them to be numerous, barbed and vary in length and thickness in relation to habitat complexity.
- c. If rictal bristles were for mechanoreception we expect them to be present in species that forage on the ground, from bark or other hard surfaces and amongst vegetation. We expect them to be longer, barbless, more numerous and flexible but this would depend on habitat complexity.

- d. If head bristles and semi-bristles are for mechanoreception we expect all hole, cavity or cave nesting Caprimulgiformes to possess long, thin bristles/semi-bristles on their face and head.

Using museum specimens and published literature on morphological and ecological attributes we assessed the relationship between rictal bristle number, length and stiffness, the presence of other facial and head bristles, and ecological parameters among the Caprimulgiformes. By phylogenetically controlled comparative analysis we show that variation in foraging and nesting ecology underlies differences among species in bristle characteristics.

6.2 MATERIAL AND METHODS

6.2.1 Morphological Measurements

We collected data on bristle characteristics from bird collections at the Natural History Museum Tring, World Museum Liverpool and Museum of Natural History, Manchester (all U.K.). Up to five members of each species were measured for rictal bristles and male and female data was pooled (in most species sexual dimorphism accounts for typically less than 5% of trait variation, Holyoak 2001). For species with distinct subspecies, specimens of the nominate species were measured but in some cases, it was necessary to pool individuals of different subspecies. If there were sufficient individuals of the different subspecies these were measured separately. Rictal bristles were counted along the right side of the bill and head and the five longest rictal bristles were measured from the base to the tip using digital callipers. The thickness of the same five rictal bristles was measured in two ways. Firstly, at the point of emergence from the skin, each bristle was measured using digital callipers and a mean taken. Where bristles were less than 0.1 mm (i.e. below the minimum measuring unit of the callipers) we assumed that they were 0.09 mm. To test our assumption about bristle width (mm) we performed a qualitative analysis by assigning each bristle a value between 1 and 4, where; 1 was very flexible, 2 was flexible, 3 was stiff and 4 very stiff. We then correlated the results finding a positive correlation

($r=0.312$, $n=79$, $p=0.009$). From this we were able to generate a measure of bristle flexibility or 'stiffness' by calculating the ratio of the bristle length:width. In all, 489 specimens constituting 83 species, of which 17 species were subdivided into 30 subspecies, were measured. High quality photographs in Cleere (2010) allowed a further seven species to be measured for rictal bristle number and length but not stiffness. The length of the bird's body in each photograph was measured and scaled-up to the average body length for the species (Holyoak 2001) giving an approximate body length and bristle length. Rictal bristle data for 16 species of Old World nightjars was taken from Jackson (2007).

Mouth area was calculated by measuring from the anterior end of the maxilla (bill tip) in a straight line along the anterior edge (tomium) of the upper mandible to the rictus. Gape width was measured as the external distance between commissural points at the rictus. These two values were multiplied giving an approximate area of the gape. Due to a unique jaw anatomy, wherein nightjar mouths open both vertically and horizontally, we expect that we have underestimated the effective area of the gape (Buhler 1970). We also collected data on the presence/absence of other types of bristle and semi-bristle (Appendix A Table 3). For categorisation we (C. L.) sketched the different types of bristle and semi-bristle in the five Caprimulgiform families included in this study (Podargidae separated into *Podargus* and *Batrachostomus*) (Figure 6.4).

Despite some of the problems associated with obtaining reliable data on mass (Rising and Summers 1989) it is conventional to use body mass for studies where interspecific size dimorphism may be of interest (e.g., Owens and Hartley, 1998). We obtained body mass and wing length data from Cleere (1998, 1999) and Holyoak (2001). For certain species only Holyoak (2001) was used because he provided means and sample sizes for subspecies. Except for mass, where this data was missing from Cleere (1998, 1999) and Holyoak (2001) these measurements were taken from the museum specimens. Where no

data on mass was available for species we estimated it from a genus level allometric equation using wing length as predictor (Appendix B1).

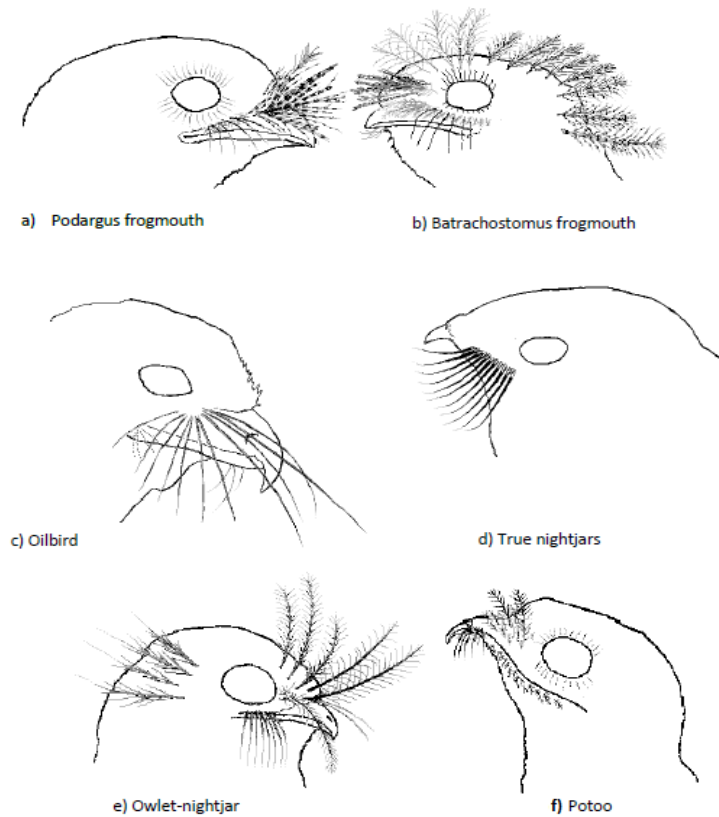


Figure 6.4 Illustrations of bristles on one side of the head of Caprimulgiformes. (See Table 3, Appendix A for occurrence of bristles and semi-bristles within the Order).

6.2.2 Foraging behaviour

Data on the foraging habits of Caprimulgiformes were gathered from the species accounts in Cleere (1998, 1999) and Holyoak (2001) and where the original data were from a single or more contemporary source this was consulted directly (Bent 1940, Fry *et al.* 1988, Jackson 2003, Pople 2003, Wilkinson 2009, Cohn-Haft and Kirwan 2012, Holyoak and Kirwan 2012, Cleere and Bonan 2013, Cleere and de Juana 2013, Cleere and Garcia 2013, Cleere and Kirwan 2012, 2013, Cleere, Kirwan and Bolan 2013, del Hoyo and Collar 2014, Holyoak and Garcia 2015). Where records could not be independently verified, we made certain assumptions. Difficulties arise when identifying nightjars in the field in low light

levels so species accounts may be inaccurate (see Jackson, 2003 for fuller treatment). However, both Holyoak (2001) and Cleere (1998) are particularly careful when recounting species accounts highlighting where mis-identification has occurred. Fieldworkers use terms such as 'night' or 'high' in general terms making it difficult to allocate activity periods or foraging habits to species and often misuse the terms, hawking and sallying. For these reasons, when categorising nightjar feeding habits, we aimed to subsume terms which were related under a unified heading or explicate the meaning of terms in specific circumstances to overcome ambiguity. For some species there were incomplete descriptions in the literature of some aspects of foraging behaviour but the following were included in statistical analysis: foraging behaviour was categorised as: *height*, devolved into 'low', 'various' (different heights including terms such as high, low, moderate and various), 'high' and 'on the ground'; *method*, categorised as 'hawking', (species that feed in continuous flight), 'sallying', (species that feed by making short flights from an elevated or terrestrial perch), 'hawking and sallying', 'sallying to ground/foilage' and 'fruit from trees'. Where no data on species' foraging ecology was available we communicated directly with fieldworkers (please see acknowledgement for the list of fieldworkers and Appendix B2 for more detail on secondary data collection).

6.2.3 Ecological attributes

The majority of Caprimulgiformes species do not defend foraging areas and therefore foraging habitat is not necessarily the same as the general habitat used for other activities, including nesting. Ecological variables of feeding habitats (those used solely for foraging - hereafter 'foraging habitat') and general habitats (those used generally for nesting and territory - hereafter 'general habitat') of Caprimulgiformes were taken from species accounts in; Cleere (1998, 1999), Holyoak (2001) and Jackson (2003, for foraging habitats only). Both general and foraging habitats were scored for structural density following Badyaev & Leaf (1997) but using finer scales taken from Pople (2003): (1) open water, sand bars, bare ground/tracks, open grasslands/savannah, steppes and deserts; (2) bushy-savannah, heathland, marshes and semi-desert; (3) scrub, open woodland and woodland

edges; (4) woodland, plantations, mangroves, scrub forest and forest clearings or edge; (5) forests; (6) caves (general habitat only for *Steatornis*). We categorised habitat on an ordinal scale so that we can use a mean habitat score for each reference source based on the range of habitats listed therein. For example, if a species is restricted to both 'scrub forest and forest clearings or edge' (4) and 'forests' (5), its mean habitat score would be 4.5. We are interested in the mean habitat complexity describing a species' range of habitats. If a species is a specialist this will be represented by its mean habitat score which is likely to be low, if it occupies only open habitats or high, if it occurs exclusively in closed habitats. If it is a specialist of semi-open habitat or a generalist it is more likely to have a middle score. Mean scores from the sources were well correlated with one another (general habitat, $r=0.90$, $n=104$, $p<0.001$; foraging habitat, $r=0.81$, $n=95$, $p<0.001$), and an average of these means was used in all analyses. General habitat and foraging habitat were also correlated with one another, albeit less strongly showing that foraging habitat is not the same as general habitat ($r=0.679$, $n=95$, $p<0.001$). The duration of twilight as well as maximum and minimum light levels varies significantly with latitude and these may have a bearing on the feeding conditions for species with different breeding ranges (Martin 1990). We calculated the midpoint (hereafter 'midrange') latitude of the breeding range of each species. In terms of nesting type we determined if species nested on the 'ground - open', 'ground or elevated - open', 'tree branch - platform', 'tree branch - depression', 'tree branch - cup', 'tree - cavity' and 'cave ledge'.

6.2.4 Phylogeny reconstruction

A composite phylogenetic tree was reconstructed from trees using different morphological and molecular markers published by Barrowclough, Groth and Mertz, (2006), Ericson *et al.* (2006), Larsen *et al.* (2007), Livezey and Zusi, (2007), Hackett *et al.* (2008), Braun and Huddleston, (2009), Mayr, (2010), Han *et al.* (2010), and Sigurðsson and Cracraft, (2014) using Mesquite (Maddison and Maddison 2011, version 2.75). For species that had not been sampled their phylogenetic affinities were assessed using Cleere (1998, 1999, 2010), Holyoak (2001), del Hoyo *et al.* (2014) and proposals by the American

Ornithologists Union and South American Ornithologists Union. The phylogeny by Sigurðsson and Cracraft, (2014) is by far the most complete and, importantly, has excellent taxon sampling of subspecies, and while we use this genus names follow Cleere, (2010) and we adopt *Gactornis* from Han *et al.* (2010) for the basal Madagascan species Collared Nightjar. We assigned branch lengths using Pagel's lambda (1992) in Mesquite version 2.75. We strove for a fully bifurcating tree but due to polytomies in published trees and incomplete phylogenetic information, where phylogenetic affinity could not be resolved with confidence, we removed the species from the tree. The final tree included 80 species, of which 17 were subdivided into 24 subspecies, from all 21 genera in the five Caprimulgiform families (Figure 6 5).

6.2.5 Data analysis

We used the PDTREE program (Midford *et al.* 2011) to convert the tree to a phylogenetic variance-covariance matrix. Data were interrogated for phylogenetic signal using the PHYSIG programme in Matlab (Garland 2009). We used Regression V2 (Lavin *et al.* 2008, Garland 2009) to evaluate hypotheses about the relationship between bristle and gape qualities and ecological variables while correcting for variation in phylogenetic relatedness between species. We examined the effects of body mass, latitude, general habitat density, foraging habitat density, foraging method, foraging height and nesting ecology on bristle number, length, stiffness and mouth area. We included body mass as a covariate. Running the main effects analyses without body mass leads does not qualitatively affect results. Data restrictions prevented us from assessing any interaction terms with more than two factors, due to too few data. Hence we generated full two factor interaction models and then reduced them down to include only significant (or nearly significant) interaction terms and main effects. Since bristle length and number are correlated we ran the analyses twice for each, with and without the other as covariate. This enables us to judge causes of variation in the trait in terms of the absolute value, and having corrected for the other term. Data (including counts of bristles etc.) were sufficiently close to a

normal distribution to not require transformation. We performed a separate analysis on the presence of different types of bristle in relation to nesting ecology.

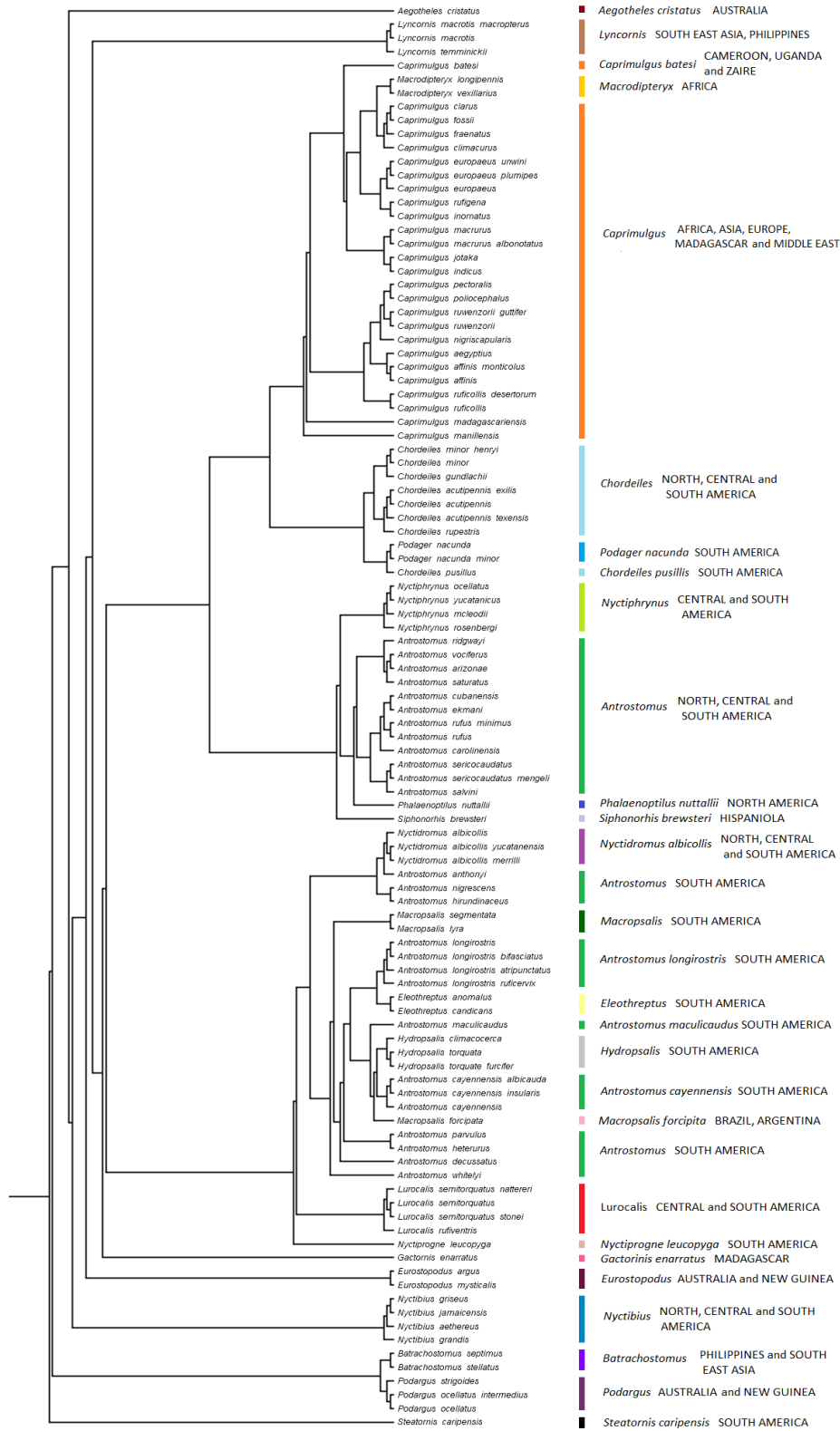


Figure 6.5 Phylogenetic relationships between the Caprimulgiformes included in this study. Tree structure is based mainly on Sigurðsson and Cracraft (2014), but genus names follow Cleere (2010).

6.3 RESULTS

The results of the statistical analyses are summarised in Tables 6.1 and 6.2. Results for the predictive variable latitude are not included because none were significant.

6.3.1 Nesting ecology

If bristles are for mechanoreception we expected that species nesting in cavities, holes or caves to be the most setose. However, nest type only significantly explained the possession of malar and loral bristles and there was a significant interaction between body mass and nest type and the presence of rictal bristles (Table 6.1). This interaction stems from species with large body masses and nesting in trees possessing both bristles and semi-bristles at their rictus; species that nest in tree cavities and on the ground possessing barbless bristles at the rictus; and small mass species nesting on the ground possessing mainly vestigial bristles. Nest type did not explain the presence of other bristles. General habitat explained the possession of crown semi-bristles but foraging habitat did not explain the presence of any bristle types as a main effect. There were significant interactions between body mass and both general and foraging habitats and the presence of rictal bristles. Mouth area did not correlate simply with body mass but there was an indication of an interaction between foraging method and mass. It seems that species that use hawking and sallying, or hawking have proportionally smaller mouths than those that sally irrespective of body mass although this is inconclusive.

Nest type appears to exert little influence over the presence of bristles except for rictal bristles so all further analyses consider rictal bristles because we want to test hypotheses about their function in relation to nesting and foraging.

6.3.2 Bristle number

We expect bristle number to vary based on whether bristles are used to capture prey, protect the eyes or aid in mechanoreception. Bristle number (without correction for

bristle length) was influenced by a significant interaction between mouth area and foraging habitat but no main effects (Table 6.2). However, when allowing for bristle length, variation in bristle number was affected by significant interactions between mouth area and each of bristle length, foraging and general habitats. Hence it is the residual bristle numbers after factoring out variation in bristle length that is most strongly affected by interactions between mouth area and habitat variables. Figure 6.6 shows that there is positive correlation between bristle length and bristle number for species with small mouths (Figure 6.6A: area less than 650mm), but in those with larger mouths there is no relationship (Figure 6.6B-D).

There were also significant main effects of foraging habitat and foraging method. Species that forage by 'sallying to ground/foilage' had a higher mean number (Figure 6.7) (mean=10.7, ± 1.8 , $n=10$) of rectal bristles than species using any other foraging method, and species that 'sally', (mean=7.7, ± 0.9 , $n=33$) and 'hawk and sally' (mean=8.5, ± 0.7 , $n=26$) had more than species that 'hawk' (mean=4.2, ± 1.7 , $n=34$). This supports our hypothesis that bristles are for protection, but may also have a mechanosensory role, when foraging in complex habitats. They do not appear to be important in prey capture.

The relationship between bristle number and mouth area is influenced by foraging habitat (Figure 6.8). At both low and high foraging densities we find animals with (vestigial) no bristles: small mouthed birds that have vestigial bristles at low densities so the correlation is positive (Figure 6.8A), but larger mouthed birds have the vestigial bristles at high densities so the correlation becomes negative (Figure 6.8D). There is no relationship between mouth area and bristle number at intermediate habitat densities. Bristle number may have a role in eye protection in dense foraging habitats but when mouths reached a certain size this function is not apparent, regardless of habitat density.

The relationship between bristle number and mouth area is affected by general habitat densities (Figure 6.9), but in this case at low densities there is an absence of bristles, and

so a positive relationship (Figure 6.9A). This suggests that bristle number is related to a mechanosensory role in dense general habitats.

6.3.3 Bristle length

As with bristle number, we predicted bristle length would vary based on whether bristles are used to capture prey, protection or mechanoreception. Including bristle number in the analysis of bristle length had no qualitative effect on the results (Table 6.2). There was an effect of foraging method: bristles are significantly shorter in hawking species than all others (Figure 6.10). There was also a main effect of foraging height because species that forage high have the shortest bristles (Figure 6.11). Bristle length is affected by an interaction between foraging habitat and mouth area (Figure 6.12). Similar to the results for bristle number there are vestigial bristles at low and high foraging habitat densities, with positive (low density, Figure 6.12A) and negative (intermediate and high foraging habitat density) correlations (Figure 6.12B-D). There was no effect of nest type on bristle length. We conclude that bristles are not used for prey capture. Bristle length is related to their role in mechanical protection in complex foraging habitats but this is affected by mouth area and we cannot rule out a mechanosensory role.

6.3.4 Bristle stiffness

We expected bristles to be stiff if they are used as ‘insect nets’ or for protection and we predicted that they would be more flexible if required for mechanoreception. Species foraging high above the ground and those foraging on the ground have substantially less stiff bristles than those foraging at low or varied levels, and those foraging low have the most stiff (Figure 6.13). Bristle stiffness is also affected by variation in foraging habitat wherein rictal bristles are finest in dense foraging habitats. Finally, there was no effect of nest type on bristle stiffness. We conclude that flexible bristles suggest a mechanosensory role in ground foragers and birds foraging in dense habitats.

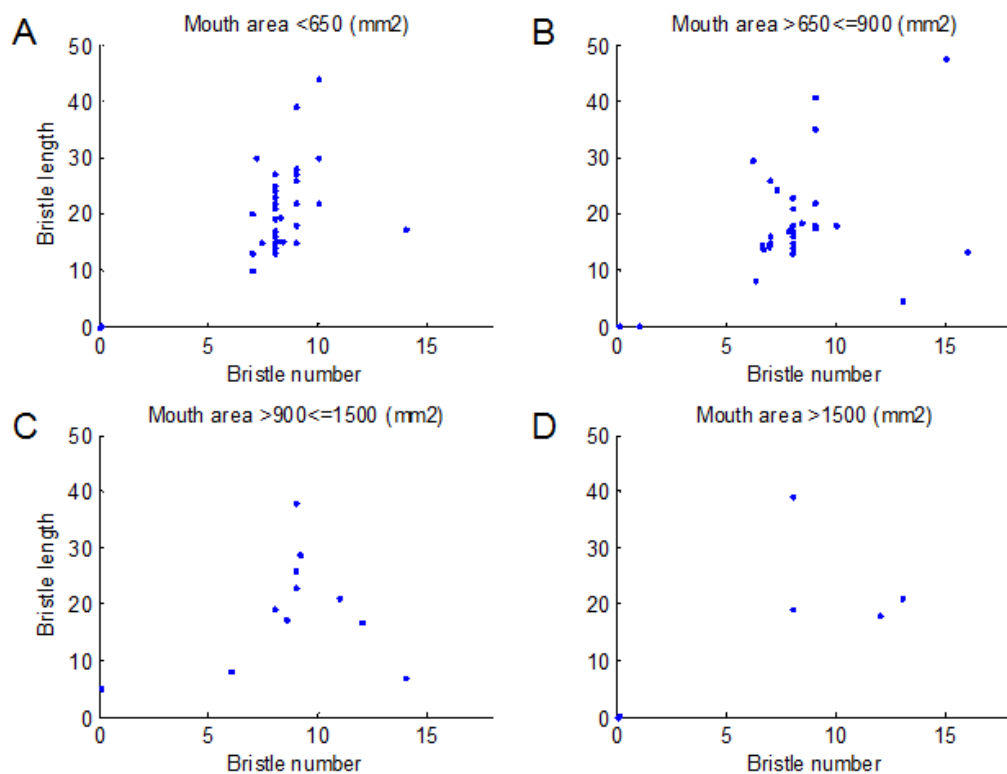


Figure 6.6 Relationship between bristle number and bristle length with interaction with mouth area.

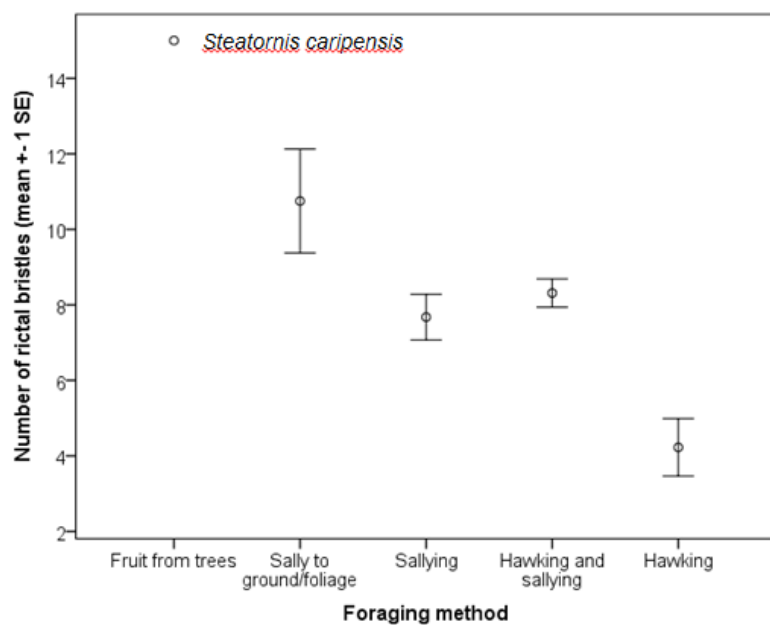


Figure 6.7 Relationship between bristle number and foraging method

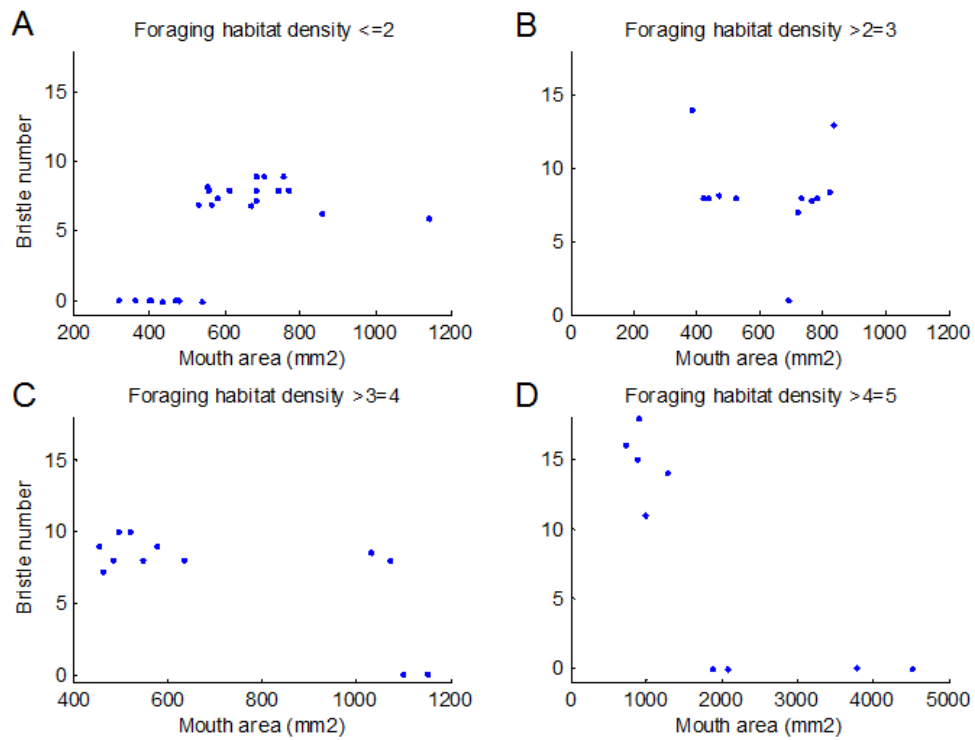


Figure 6.8 Relationship between mouth area and bristle number with interaction with foraging habitat density.

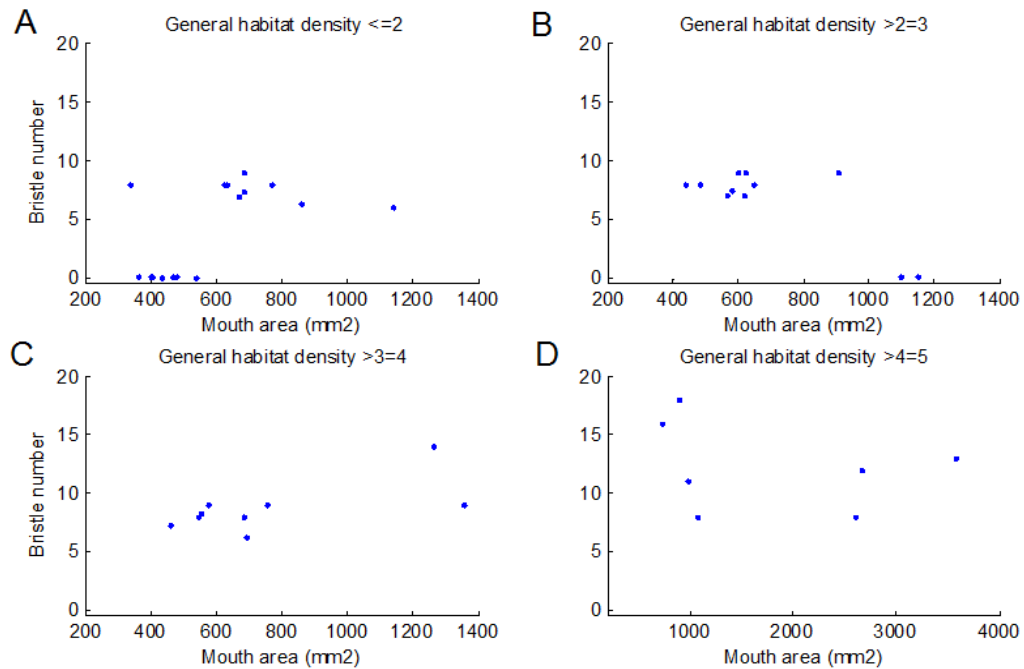


Figure 6.9 Relationship between bristle number and mouth area with interaction with general habitat density.

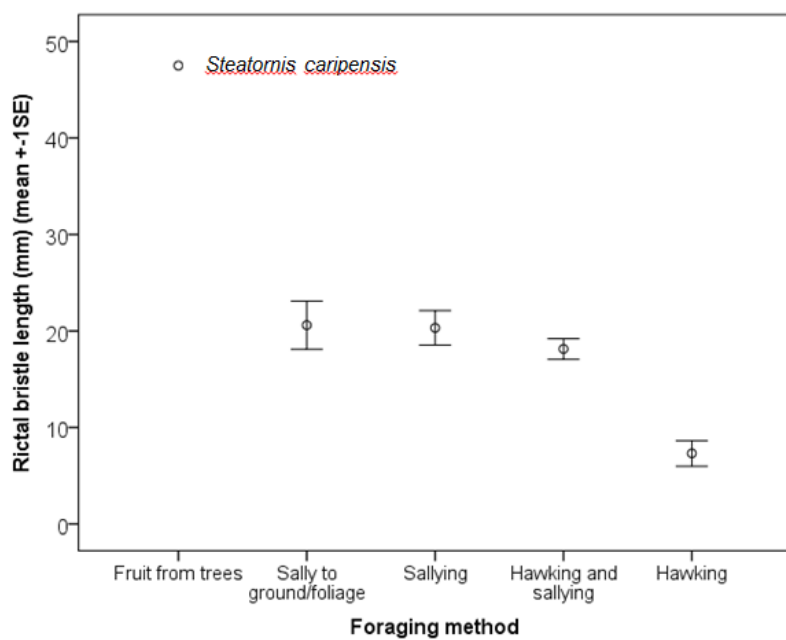


Figure 6.10 Mean (± 1 SE) length of rictal bristles in relation to foraging method.

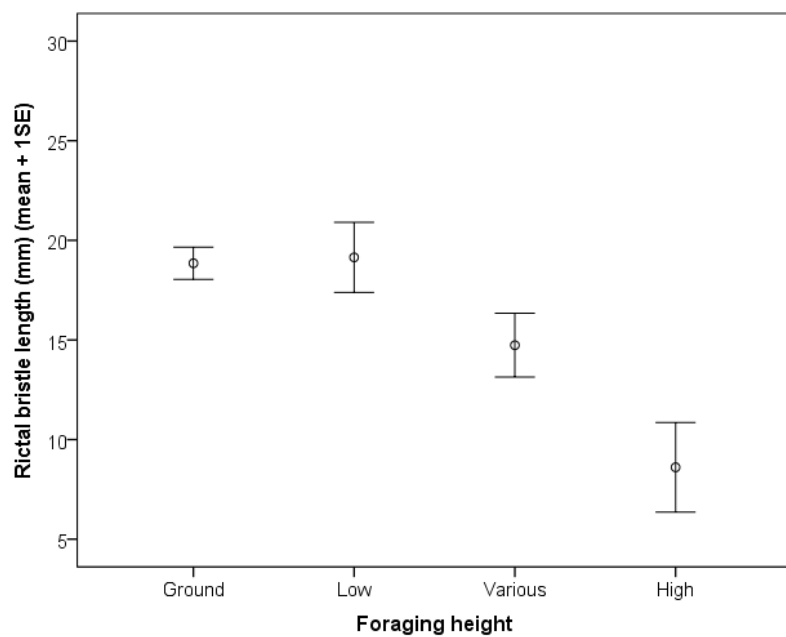


Figure 6.11 Mean (± 1 SE) length of rictal bristles in relation to foraging height.

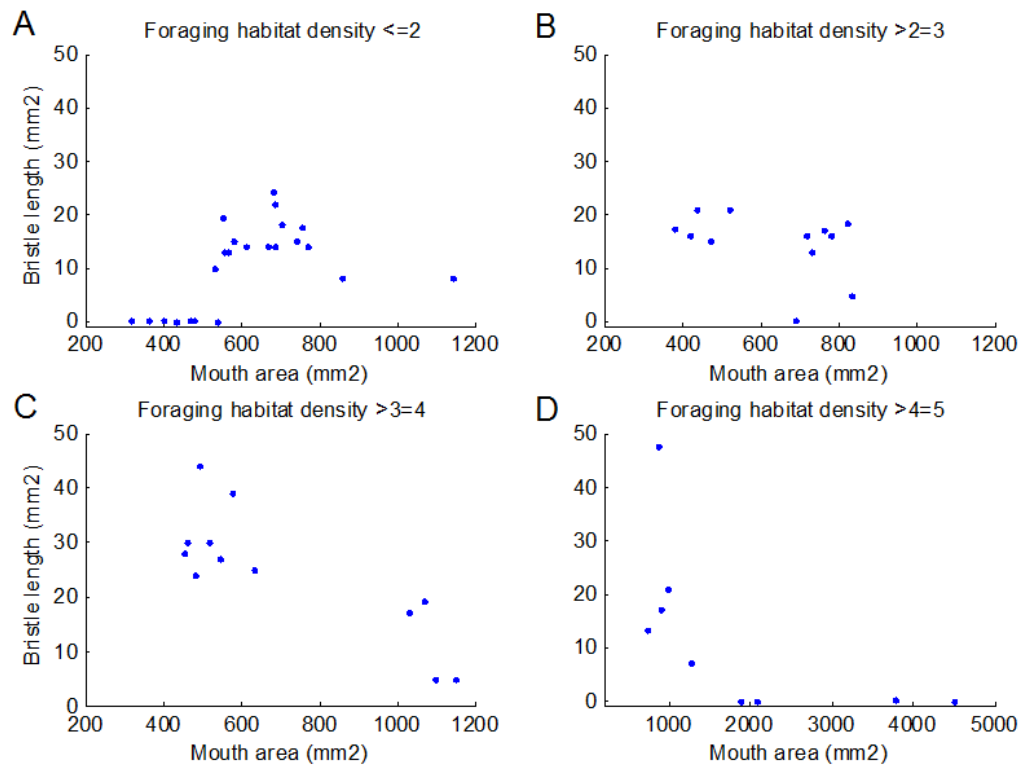


Figure 6.12 Relationship between rictal bristle length and mouth area in relation to the interaction with foraging habitat density.

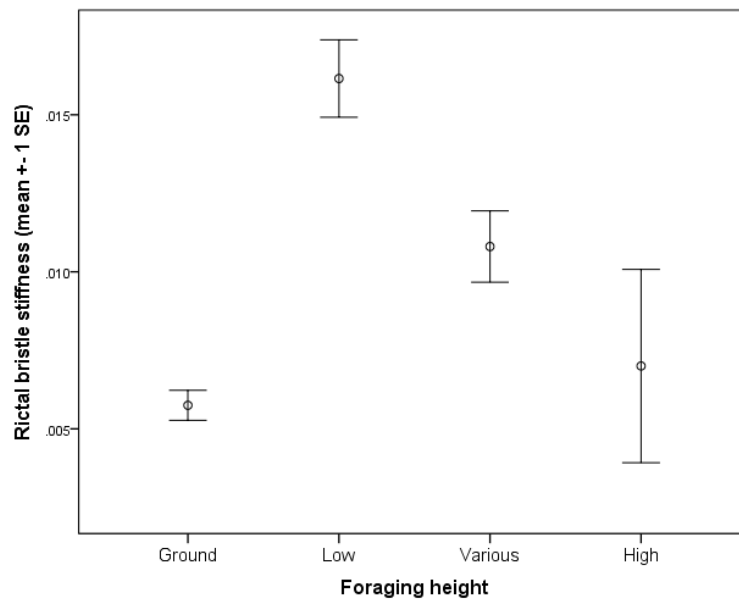


Figure 6.13 Mean (\pm 1 SE) rictal bristle stiffness in relation to foraging height.

Table 6.1 Summary of models and interaction terms for effects of mass, nest type and habitat complexity on all facial bristles. *denotes significant effect/interaction. All interactions are included. '+/-' indicates the direction of the effect d. In the text we report analysis of these variables alone.

	Rictal				Basal				Naral				Loral				Ear Coverts				Malar				Eyelash				Interramal				Forehead				Crown			
<i>Continuous variables</i>	<i>d</i>	<i>t</i>	<i>df</i>	<i>p</i> ≤	<i>d</i>	<i>t</i>	<i>df</i>	<i>p</i> ≤	<i>d</i>	<i>t</i>	<i>df</i>	<i>p</i> ≤	<i>d</i>	<i>t</i>	<i>df</i>	<i>p</i> ≤	<i>d</i>	<i>t</i>	<i>df</i>	<i>p</i> ≤	<i>d</i>	<i>t</i>	<i>df</i>	<i>p</i> ≤	<i>d</i>	<i>t</i>	<i>df</i>	<i>p</i> ≤	<i>d</i>	<i>t</i>	<i>df</i>	<i>p</i> ≤	<i>d</i>	<i>t</i>	<i>df</i>	<i>p</i> ≤				
Mass	+	3.5	88	0.01*	+	0.7	89	0.48	-	0.6	90		+	0.9	89	0.36	-	0.05	90	0.86	-	1.1	90	0.28	+	1.8	89	0.07	+	0.1	90	0.91	-	1.1	89		0.4	89		
									0.55																										0.28		0.66			
General Habitat	+	0.23	89	0.81	+	0.2	90	0.98	+	0.31	89		+	0.58	88	0.56	-	0.99	89	0.32	+	0.05	90	0.95	+	0.5	88	0.61	+	0.22	89	0.83	+	0.3	86		2.6	89		
									0.76																										0.75		0.01*			
Foraging Habitat	-	0.68	86	0.49	+	0.52	86	0.6	+	0.19	87		+	0.52	88	0.60	+	0.19	88	0.84	-	0.3	88	0.75	+	0.66	87	0.50	+	1.4	88	0.16	+	0.03	87		1.4	87		
									0.85																										0.97		0.15			
<i>Categorical variables</i>	<i>f</i>	<i>df</i> 1/2		<i>p</i> ≤	<i>f</i>	<i>df</i> 1/2		<i>p</i> ≤	<i>f</i>	<i>df</i> 1/2		<i>p</i> ≤	<i>f</i>	<i>df</i> 1/2		<i>p</i> ≤	<i>f</i>	<i>df</i> 1/2		<i>p</i> ≤	<i>f</i>	<i>df</i> 1/2		<i>p</i> ≤	<i>f</i>	<i>df</i> 1/2		<i>p</i> ≤	<i>f</i>	<i>df</i> 1/2		<i>p</i> ≤	<i>f</i>	<i>df</i> 1/2		<i>p</i> ≤				
Nest type	1.8	6/86		0.08	0.9	6/87		0.38	0.1	6/88		0.89	2.1	6/87		0.031*	1.5	6/88		0.14	2.3	6/88		0.02*	1.4	6/87		0.16	1.6	6/88		0.12	1.2	6/87		0.23	0.2	6/87		0.78
<i>Interactions</i>	<i>t</i>	<i>p</i> ≤			<i>t</i>	<i>p</i> ≤			<i>t</i>	<i>p</i> ≤			<i>t</i>	<i>p</i> ≤			<i>t</i>	<i>p</i> ≤			<i>t</i>	<i>p</i> ≤			<i>t</i>	<i>p</i> ≤			<i>t</i>	<i>p</i> ≤			<i>t</i>	<i>p</i> ≤						
Mass & Nest type	3.8	0.001*			0.7	0.47			0.6	0.53			0.7	0.47			0.5	0.59			0.9	0.37			1.5	0.12			0.9	0.36			1	0.31			0.6	0.58		
Mass & General Habitat	3	0.002*			0.46	0.65			0.04	0.96			0.44	0.66			0.98	0.32			0.25	0.80			0.65	0.51			1.48	0.14			0.16	0.87			0.75	0.40		
Mass & Foraging Habitat	3.2	0.002*			0.63	0.53			0.5	0.61			0.63	0.53			0.33	0.69			0.23	0.82			1.8	0.28			0.71	0.47			0.59	0.56			0.76	0.44		

Table 6.2 Summary of models and interaction terms for effects of explanatory variables on rictal bristles. *denotes significant effect. ** indicates when the trait was included in the model as an independent variable. Significant and selected non-significant interactions are included. '+/-' indicates the direction of the effect d. '-' indicates that the model would not run with this variable incorporated and in the text we report analyses of these variables alone.

					Bristle Number (with								Bristle length (with															
	Bristle Number				bristle length)**				Bristle length				bristle number)**				Bristle stiffness				Mouth area				Mass			
Continuous variables	d	t	df	p≤	d	t	df	p≤	d	t	df	p≤	d	t	df	p≤	d	t	df	p≤	d	t	df	p≤	d	t	df	p≤
Mass	+	0.95	86	0.35	+	0.53	86	0.62	-	0.85	85	0.68	-	0.63	85	0.84	-	0.17	65	0.87	+	10.1	85	0.001*	-	-	-	-
Mouth area	+	1.03	86	0.31	+	0.6	86	0.55	+	2.52	85	0.014*	+	2.08	85	0.041*	-	0.99	65	0.328	-	-	-	-	-	-	-	-
Foraging habitat	+	1.16	86	0.25	+	2.5	86	0.02*	+	0.64	85	0.523	+	1.68	85	0.097	-	2.35	65	0.02*	+	1.09	85	0.29	-	0.37	85	0.55
General habitat	-	0.67	86	0.5	-	1.07	86	0.29	+	0.03	85	0.87	+	0.22	85	0.83	+	0.57	65	0.57	+	0.13	85	0.87	+	1.76	85	0.082

6.4 DISCUSSION

A major aim of this paper is to evaluate how habitat characteristics, especially those related to nesting and foraging, correlate with systematic variation in important morphological traits, rictal bristles and mouth architecture. We predicted that rictal bristles of aerial insectivores would be short, stiff and barbed, due to their putative ‘insect net’ role. Contrary to our prediction rictal bristles were vestigial in *Nyctibius*, *Eurostopodus*, *Lyncornis*, *Chordeiles*, *Lurocalis* and *Nyctiprogne* but were prevalent in all other aerial insectivores where they varied in character. If rictal bristles were used to detect movement of prey in the bill, or the position of prey at close quarters, we would expect them to be functional in all aerial insectivores but they were not. We therefore agree with our second hypothesis, that rictal bristles are required for head protection from prey and hard surfaces in aerial insectivores. Bristles were the least flexible in species that forage low and we presume this is for protection. We also predicted that they would be longer, more flexible and more numerous if they had a mechanosensory role. In agreement with our prediction, we found that they were more numerous and more flexible in species that sally to the ground. They were equally flexible in species that forage at high levels but they are vestigial in most species in this group. We conclude they may have a dual role of protection and mechanoreception in species foraging in complex habitats where risk of collision and injury is more likely. After controlling for body mass and phylogeny there was little evidence to support our final hypothesis that face and head bristles are used for mechanoreception in hole and cavity nesting species, although we cannot rule this out. Our analyses showed that the number, length and stiffness of rictal bristles are all affected by interactions between mouth area and the foraging and general habitat of species. Our results have important implications for understanding the function and of evolution of these poorly understood structures in these birds, and potentially other species. We will describe each of the traits we investigated, providing explanations for their occurrence and function.

This assessment enables us to provide an evolutionary perspective on the origin of bristles, their current phylogenetic distribution and their importance in nightjar radiations, and their implications for understanding the evolution of morphology in birds.

6.4.1 Ecological Determinants of Morphology

6.4.1.i Bristle number

The number of bristles increases with bristle length in guilds with small gapes. This relationship was driven by the fact that bristles are vestigial in very small-mouthed species foraging in open habitats and very large-mouthed species feeding in dense habitats. This suggests that bristles are required for protection (e.g., Kuster 1905, Conover and Miller 1980) but not to enhance prey capture (e.g., Welty 1962) in small-mouthed species foraging in open habitats and in large mouthed species foraging in dense habitats. In contrast, only in low density general habitats we found vestigial bristles suggesting that at all other habitat densities rictal bristles are required to protect delicate head structures (e.g., Jackson 2007).

The significant main effect of foraging method on bristle number arises from species using a foraging method of ‘sallying to ground/foilage’ which had a higher mean number of rictal bristles than species using any other foraging method and ‘sallying’, and ‘hawking and sallying’ species had more than ‘hawking’ species. This model would not run with foraging height included with foraging method (there were too many incomplete cells in the data matrix), however, when foraging height was included as a single main effect it explained the variation in bristle number and showed that species that foraged ‘high’ had fewer bristles than other guilds. Due to reduced light levels associated with cluttered environments and the requirement for a perch, sallying species may be more likely to collide with vegetation or sustain injury from prey when foraging. In contrast, hawking species, such as the nighthawks and eared-nightjars, tend to fly at higher levels (Bent 1940, Holyoak 2001) and thereby largely avoid contact with vegetation and prey detection might be easier (Brigham and Barclay 1995).

To our knowledge, no study has systematically related bristle number to an ecological attribute. It would appear that the development of rictal bristles in nightjars that feed by 'sallying to ground/foilage', 'sallying' and 'hawking and sallying' might be for eye and head protection from prey and vegetation in foraging habitats which are complex. Hawking species had fewer bristles than species using any other foraging method. We conclude that bristle number increases in dense general habitats and at intermediate densities in foraging habitats for head protection (e.g., Lederer 1976) but this is affected by mouth area and foraging method. Analysis also showed that nesting ecology had no effect on the number of rictal bristles supporting observations above that rictal bristles are adaptations for protection during foraging (e.g., Chandler 1914, Dyer 1976).

6.4.1.ii Bristle length

There was an effect of foraging method and foraging height on bristle length showing that species that used 'sallying', 'hawking and sallying' and 'sallying, to ground/foilage' as their main feeding method, and those that foraging low or at various heights possessed longer mean rictal bristles than species that forage by hawking high above the ground. As highlighted above, such species include the nighthawks which forage up to 175 meters above the ground (Holyoak 2001), and absence of functional bristles in this family suggests that in setose species bristles are not employed for prey capture (e.g., Van Tyne and Berger 1965, Conover and Miller 1980) but might be required for mechanical protection (e.g., Chandler 1914, Brush 1967, Dyer 1976, Martin 1990). We also found that bristle length increases with foraging habitat density but this is affected by mouth area wherein when mouth area is greater than 1000 cm² bristle length decreases regardless of foraging habitat density. This suggests that long bristles in dense foraging habitats might allow birds to 'sense' the proximity of obstacles such as vegetation whilst foraging but when mouth area reaches a certain size or when birds forage high above the ground selection for long bristles weakens. The long bristles found in the oilbird (*Steatornis*

caripensis) might protect facial plumage from contamination by fruit juices and this supports hypotheses about their function in raptors (Chandler 1914).

Our findings support studies by Jackson (2007) on Afrotropical nightjars in which he found that species feeding in closed habitats possessed longer rictal bristles (mean = 20.2mm) compared with species which forage in open habitat (mean = 18.3mm). He did not relate this to foraging method. However, in a review of foraging behaviour he suggested that the lower foraging luminosity associated with 'closed' habitats necessitated greater eye protection and hence longer bristles (Jackson 2003). Our findings also support the general observation that aerial-insect-foragers possess long rictal bristles (e.g., Dyer 1976, Leisler and Winkler 1985, Keast and Sanders 1991) but none of these studies examined habitat complexity. However, Landmann and Winding, (1993) specifically looked at habitat complexity and found that species of Turdidae which preferably foraged by aerial hawking or flycatching in more open areas have long rictal bristles whereas those feeding pedally (on foot) in closed habitats lacked bristles. This suggests that in diurnal species rictal bristles are important in eye protection during aerial foraging but are not required for this function in ground foragers. We suggest that long bristles in dense foraging habitats act like mammalian vibrissae or head plumes (Seneviratne & Jones 2008, 2010) allowing the birds to sense the proximity of hard surfaces and this is particularly important in scotopic conditions of nocturnal organisms where visual acuity might be reduced. However, when mouth area reaches a certain size bristles are no longer required for this function in large mouthed aerial foragers such as the potoos (Nyctibiidae) but remain functional in the ground feeding frogmouths (*Podargus*). As with bristle number, our analysis showed that nesting ecology had no effect on the length, providing further support to our findings that rictal bristles are adaptations for foraging (e.g., Lederer 1972, Conover and Miller 1980).

6.4.1.iii Bristle stiffness

Foraging habitat density explained the variation in bristle stiffness resulting in a negative correlation. Foraging height also affected bristle stiffness and showed that ground feeding

species and those which feed at high levels (in which bristles are largely vestigial) had significantly finer bristles than species feeding at other heights. The model would not run with foraging method included with foraging height (there were too many incomplete cells in the data matrix), however, when foraging method was included as a single main effect it explained the variation in bristle stiffness showing that hawking species and those that sally to the ground/foilage have the most flexible bristles. This suggests that functionally finer bristles might be more sensitive for detecting obstacles (Cunningham *et al.* 2011) in a cluttered foraging habitat when a bird is foraging and in particular on the ground and this may certainly apply to the ground feeding frogmouth, *Podargus strigoides*, which we studied. We suggest that bristle stiffness is affected by their tactile role (Kuster 1905, Lucas and Stettenheim 1972, Cunningham *et al.* 2011) and the more volant species feeding low possessed stiffer bristles for eye protection from prey or vegetation when feeding (Dyer 1976, Conover and Miller 1980, Cunningham *et al.* 2011). In our study, bristle stiffness was negatively correlated with body mass. However, due to isometric scaling of the bristle base with mass there may be constraints of a minimum requirement for a certain width that does not increase as the length of the bristle increases.

In conclusion, finer bristles might have an enhanced mechanosensory function in ground feeding species and might be the outcome of weakened selection in those species foraging high above the ground, in which they are often rudimentary. Nest type had no effect on bristle stiffness so it appears that bristles are not required for mechanoreception in enclosed nests. .

6.4.2 Nesting ecology

Analysis of the variation in the presence of different types of head bristle in relation to nesting ecology showed that only malar and loreal bristles were affected by nest type. Possession of malar and loreal bristles and semi-bristles is negatively correlated with nest openness wherein only cavity nesting species possess malar bristles and only those

species nesting in trees on platforms, cups or depressions possess loreal bristles. There was a significant interaction between body mass and nest type and the presence of rictal bristles but this relationship was unclear. Visual analysis (Appendix A, Table 3) shows that species that nest in trees, frogmouths, owl-nightjars and to a lesser extent the potoos, possess bristles and semi-bristles (Figure 6.1 *a, b, c, d, e, f, and h*) on various regions of the head (Figure 6.4 *a, b, e, f*) whereas the ground nesting true nightjars only possess rictal bristles in the majority of species (Figure 6.1 *f, g*, Fig. 4 *d*). Members of the cavity nesting owl-nightjars are the most setose family in the Order (Figure 6.4 *e*) and presence of malar semi-bristles (Figure 6.1 *b*) does appear to be related to this nesting habitat. It is likely that a greater range of bristles and semi-bristles, and in particular, those at the malar and loreal region, affords head protection for species which are arboreal nesters and these might have a secondary function when foraging on the ground. The retention or development of face and head bristles, along with semi-bristles and modified feathers, may therefore have a mechanosensory role in the cavernicolous oilbird (Figure 6.1 *f*, Figure 6.4 *c*), and frogmouths (Figure 6.1. *a, b*, Figure 6.4 *a* and *b*). We propose an additional hypothesis that face and head bristles may enhance crypsis in Podargidae and Nyctibiidae when the birds are roosting by disrupting the outline of the head (Lorek 1992, Galeotti and Rubolini 2007). The arrangement of the elaborate semi-bristles in the large frogmouth *Batrachostomus auritus* may suggest a role in display and may be sexually selected but this has not been investigated.

6.4.3 Diversification in Relation to Habitat Switches

Both niche specialisation (e.g., Belmaker, Sekercioglu and Jetz 2011), and generalist feeding habits (e.g., Owens, Bennett and Harvey 1999) have been shown to be important in diversification among birds. It would seem that anatomical changes in feeding apparatus, namely bristle characteristics and mouth size, associated with specialisation or generalisation in foraging habitat niche and foraging method have also been important in diversification within the Caprimulgiformes. Such phenotypic adaptation to ecological shifts has also been demonstrated in the adaptive radiations of other bird groups; e.g.,

ovenbird-woodcreeper family (Irestedt *et al.* 2009) and the tyrant flycatchers (Ohlson, Fjeldsa and Ericson, 2007).

Modification of trophic adaptations associated with feeding ecology may have led to evolutionary transitions among feeding styles and habitats in Caprimulgiformes leading to niche expansion, which in turn may have led to adaptive radiations (e.g., Ohlson, Fjeldsa and Ericson 2007, Irestedt *et al.* 2009). There appears to have been a series of foraging and habitat transitions which occurred multiple times in two of the three New World radiations, apart from the Chordeilinae one, and the single Old World radiation suggesting this has been important in nightjar speciation (Figure 2). At the level of Family this transition has been from largely forest-dwelling, sallying, ground and foliage feeding frogmouths and owlet-nightjars, which are very setose and potoos, which largely lack bristles and sally into the air, to woodland and semi-open habitat eared-nightjars which predominantly hawk and possess vestigial bristles. Within the Caprimulginae the transition from forest to more open habitats continues with for example, the basal Madagascan endemic, *Gactornis ennarratus*. Many New World *Antrorstomus* species also made this habitat switch and forage by sallying and hawking in ecotone between habitats. Finally, genera such as *Eleothreptus* became open habitat specialists, whilst others such as *Nyctiphrynus* colonised dense habitats. These habitat transitions were associated with retention, and in some cases modification of, rictal bristles. For example, the poorwills, *Siphonorhis* and *Nyctiphrynus* have very long flexible rictal bristles and both genera are associated with arid lowland wooded habitats, and in these species rictal bristles may have a dual role for protection and mechanoreception. In contrast, the Chordeilinae nighthawks are the only radiation in which this broad transition is not apparent as all *Chordeiles* occupy a single open habitat niche in lowlands and forage by hawking so selection for bristles has weakened and they have become largely vestigial. Finally, the switch from denser to more open habitats can also be seen in the Old World nightjars from the largely forest dwelling *Caprimulgus manillensis*, to ecotone sallying/hawking species of *Caprimulgus* nightjars, followed by a reversion to more closed habitats. The

generalist ‘sally-hawkers’ that occupy semi-open habitat have developed shorter and stiffer rectal bristles, than their forest counterparts, and these probably provide protection for head structures and have little mechanosensory function. These habitat shifts have been demonstrated by a detailed ancestral trait reconstruction by Sigurðsson (2013) who concluded that the ancestral habitat for the Caprimulgidae was forest in northern South America, so we can conclude that bristles are ancestral. Such habitat and feeding switches have been shown to be important in speciation in other bird groups including tyrant flycatchers. The pipromorphines and elaeniines possess very similar morphology and exploit a restricted range of microhabitats associated with a gleaning foraging method, whereas the myiarchine–tyrannine–fluvicoline clade is more diverse in these respects. This greater ecological diversity appears to be connected to a greater adaptive flexibility of the search-and-sally foraging behaviour (Ohlson, Fjeldsa and Ericson 2007).

6.4.4 Conclusion: Bristles and the Evolutionary History of Nightjars

Caprimulgiformes are descended from a New World forest dwelling ancestor that possessed bristles or semi-bristles and was likely nocturnal. The relictual distribution of the oilbird, frogmouths and potoos as demonstrated by the fossil record support this (Holyoak 2001, Mayr 2009, Nesbitt, Ksepka and Clarke 2011). Ancestral diet is less easy to determine. The heavy bill morphology of the early branching extant Caprimulgiformes would suggest omnivory as the ancestral condition. Both the fossil record and pollen analyses show that a climate shift resulted in a more or less continuous cooling and drying of the planet and retraction of the tropical forests and woodlands and replacement by grassland during the late Eocene ~40 mya (Zachos *et al.* 2001). This change towards dryer and cooler ecosystems allowed the appearance of open matrices in the dense tropical forest and the creation of ecotones between complex and open habitats and this was particularly marked during the late Miocene as climatic cooling continued (10 MYA) (Latorre *et al.* 1997).

It is likely that all extant nightjar species evolved during this period independently in several different subclades in the 4 main clades. Although these radiations may not necessarily coincide with the spread of open habitat, this can be explained by the global and temporal variation in these evolutionary and ecological events which has been proposed as the reason for the lack of calibration between the spread of grasslands and the evolution of grazing animals (Pérez-Barbería, Gordon and Nores 2001, Strömberg 2005, 2011) and birds (e.g., Ohlson, Fjeldsa and Ericson 2008). Many components of nightjar morphology have subsequently been retained which demonstrates both the success of their body plan and behaviour but also the ecological limitations of their dietary niche (Martin 1990, Jetz, Steffen and Linsenmair 2003). Remaining cryptic and nocturnal in open habitats may have reduced predation pressure and competition for food with diurnal species but placed other pressures on various components of the animals to evolve. Bristles appear to be one such component and their diversification in tandem with colonisation of new habitats might have made nightjars one of the most successful groups of nocturnal birds.

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APPENDIX A

(Sub)Family	Steatornithidae	Podargidae		Nyctibiidae	Caprimulginae	Chordeilinae	Aegothelidae
Genus	<i>Steatornis</i>	<i>Podargus</i>	<i>Batrachostomus</i>	<i>Nyctibius</i>	<i>Phalaenoptilus</i> <i>Siphonorhis</i> <i>Nyctiphrynus</i> , <i>Nyctidromus</i> , <i>Antrostomus</i> , <i>Hydropsalis</i> , <i>Macropsalis</i> , <i>Eleothreptus</i> , <i>Caprimulgus</i> , <i>Macrodipteryx</i>	<i>Chordeiles</i> , <i>Podager</i> , <i>Lurocalis</i> , <i>Nyctiprogne</i>	<i>Aegotheles</i>
Rictus	BR	BR/SB	BR/SB	V	V/BR/SB	V/BR	BR
Basal	BR	SB	SB	SB	NO	NO	SB
Nares	NO	SB	SB	NO	NO	NO	NO
Lores	BR	SB	SB	SB	NO	NO	SB
Malar	NO	NO	NO	NO	NO	NO	SB
Ear coverts	NO	NO	SB	NO	SB	NO	SB
Eye	BR	BR	BR	SB	BR	NO	NO
Inter- ammus	BR	NO	BR	BR	NO	NO	BR
Forehead ¹	NO	SB	SB	NO	NO	NO	SB
Crown ²	NO	NO	SB	NO	NO	NO	SB
Diet	Fruit	Invertebrates and small vertebrates	Invertebrates	Invertebrates (rarely small vertebrates)	Invertebrates (rarely small vertebrates)	Invertebrates	Invertebrates
Foraging method	Pluck fruit from branch	Sally ³ from arboreal perch to ground, trunk, branches and foliage (rarely into air)	Sally from arboreal perch to ground, branches and foliage (sometimes into air)	Sally from arboreal perch into air	Hawk ⁴ and sally (rarely ground)	Hawk (occasionally sallying)	Sally into air or to tree trunk (rarely ground)
Foraging habitat	Forest woodland and	Forest, and woodland edge	Forest	Forest and woodland edge	Forest to open habitats	Open habitats	Forest and woodland edge
Foraging height	Various	Ground and low	Ground and low	Low and various	Low, various and high	Various and high	Low and moderate
General habitat	Caves	Forest, woodland and open woodland	Forest	Forest, woodland and open woodland	Forest to desert	Open to semi-open habitats	Forest and woodland

Nest type	Cave ledge	Tree-open platform	Tree – open cup	Tree-open depression	Ground - open (except <i>Lurocalis semitorquatus</i>)	Ground elevated open/ Tree-open depression	Tree – cavity
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Table S6.3. Qualitative assessment of bristle (BR) and semi-bristle (SB) occurrence, and absence (NO) in relation to nesting and foraging ecology in the Caprimulgiformes. Bristles or semi-bristles present but vestigial (V). This assessment shows that species that nest in trees, frogmouths, owl-nightjars and to a lesser extent the potoos, possess bristles (BR) and semi-bristles (SB) on various regions of the head, whereas the ground nesting nightjars only possess rictal bristles (BR) in the majority of species. These are vestigial in eared-nightjars and Chordeilinae except *Podager*. Member of the cavity nesting owl-nightjars are the most setose family in the Order. ¹Forehead and between eyes. ²Crown and nape. ³Sally (species that feed by making short flights from an elevated or terrestrial perch). ⁴Hawk (species that feed in continuous flight).

APPENDIX B

1. Calculation of body mass estimated from a genus level allometric equation using wing length as predictor

Antrostomus species - $=10^{(2.406 \cdot F8 - 3.6122)}$

Caprimulgus species - $=10^{(1.812 \cdot F24 - 2.2582)}$

Chordeiles species - $=10^{(1.6653 \cdot F51 - 1.9576)}$

Lurocalis species - $=10^{(2.5811 \cdot F68 - 4.0848)}$

Nyctidromus - $=10^{(2.5088 \cdot F81 - 3.7349)}$

Podargus species - $=10^{(3.2874 \cdot F91 - 5.4819)}$

F=LOG(wing length)

CHAPTER SEVEN

7.1 DISCUSSION

7.1.1 Summary of key findings

This thesis had two broad aims; firstly, to understand the factors affecting nest predation in nightjars breeding in commercial pine plantations and secondly, to produce a phylogenetic hypothesis for the family Caprimulgidae and to determine the function of a common morphological feature, facial bristles. I did this using a range of techniques, including extensive fieldwork, territory mapping, radio telemetry, artificial nests, blood sampling, molecular techniques, and appropriate analytical methods. This approach yielded robust, detailed and novel information, adding to the current understanding of the nesting ecology of the nightjar, and the systematics and evolution of these enigmatic night birds.

7.1.1.i Chapter TWO

This is the first study to quantify the effects of the research methodology on nightjars and at the time of completion, was ahead of the field in terms of questioning the welfare impacts of commonly used field techniques - e.g., Ibáñez-Álamo *et al.* (2012) - researcher disturbance on nest success, Spotswood *et al.* (2011) consequences of mist-netting, Sheldon *et al.* (2008), effects of blood sampling and Barron *et al.* (2010), effects of fitting devices to wild animals. Although mist netting and radio telemetry have been used on nightjars for nearly 20 years, with no reported effects, this was the first time that blood sampling had taken place. None of the methods used in this study had measurable long term effects on nightjars and although samples were small breeding success and return rates were comparable between sampled and unsampled birds. All of the above methods involved close contact with the birds and the significance of the effects of human disturbance are reported below. Despite these findings, I strongly advocate that the welfare of the study organism is paramount in such ecological research and unless one

conducts experiments to evaluate research effects one cannot arrive at an acceptable level of risk for such research (Wilson and McMahon, 2006).

7.1.1.ii Chapter THREE

This is the first time that such a detailed analysis of song territory attributes has been completed at different spatial scales, i.e. first order (nest site) and third order (territory) (Johnson 1980) and in relation to breeding status and related to the nesting success of this species. Observations on the behaviour of radio tagged males revealed that their breeding status can be established without finding their nest site. Mated and unmated males had similarly sized song territories and this was recorded by Sharps *et al.* (2015) but those of mated males were more compact. Air space above song territories and even song posts were shared by territorial males (Sharps *et al.* 2015). These two findings have implications for conducting accurate censuses of nightjars where population density is sufficiently high for overlaps to occur. Finally, the sex ratio for males and females was skewed and the likelihood of both sexes finding a mate might be reduced. In nightjar populations where suitable habitat is available it might be the shortage of females that is impeding occupation. This finding has implications for decision making and for prioritising management resources.

Nightjars nested in a range of habitats but most occurred on clearfells, <4 year plantations, 4-9 year plantations and heathland and these findings are in agreement with the majority of studies (e.g., Bowden and Green 2001; Cross *et al.* 2005). Within these habitats territories and nests sites of males varied significantly in area, vegetation density and vegetation height but not in compactness ratio, distance to edge, edge type, alternative nest sites or vegetation cover above the nest. Compared to random nests and territories there were significant differences in all the variables but this varied by habitat category and showed that nightjars nest closer to soft edges than would be expected by chance, avoided nesting adjacent to hard edges and nested in vegetation of intermediate density within the range available. It appears that nightjars require a balance between

nest concealment and vigilance, and also require compact territories locating the nest adjacent to soft edges. This detailed analysis of song territory and nest site, and comparison with random nests, provides a more detailed understanding of habitat selection in nightjars nesting in mixed heath-pine habitats.

7.1.1.iii Chapter FOUR

For the first time, a detailed analysis of nest success in relation to song territory attributes has been completed. Analysis showed that habitat was the single best predictor of variation in depredation, along with edge type and visit status. In terms of the different habitats depredation was significantly higher on nests in grass and bracken clearfells, and lowest in 4-9 year plantations and heathlands. Both nightjar and artificial nests adjacent to hard edges were significantly more likely to be depredated. Nest visitation had a positive effect on nest success of artificial nests. Variation in daily survival rate (DSR) was explained by territory area and compactness ratio, edge type, and vegetation density. Nests were depredated more rapidly in large territories and when adjacent to hard edges. In contrast, nest survival increased in tandem with increased vegetation density and territory compactness ratio. Depredation on artificial nests was not significantly different to nightjar nests, suggesting that predators were responding to them equally. However, predation of nightjar and quail nests was mainly avian, whereas mammals accounted for the majority predation of artificial nests containing a plasticine egg. In agreement with other studies (e.g., Villard and Part 2004), artificial nests are useful for studying predation when the population density of the study organism is low and the species is difficult to study but findings from such studies might not be generalisable. However, these results identify the importance of predator avoidance in habitat selection in this species and this might have important implications for species conservation initiatives. Such initiatives in commercial pine plantations have to meet sometimes competing demands. In plantations, hard edges are ubiquitous and unavoidable where stands of differently aged trees abut against clearfell and heathland. Nightjars seem to avoid nesting adjacent to such edges

and forest management that can factor this in will increase the ‘available’ habitat for its nightjar population.

7.1.1.iv Chapter FIVE

For the first time, a detailed family specific phylogeny has been produced for the nightjars, with the main conclusion that *Caprimulgus* is not monophyletic. We also found strong biogeographical structuring within the Caprimulgidae that contain four geographically isolated clades. One of these clades contained just *Chordeiles* species and is restricted to North and Central America. However, the remaining three clades each contained a mixture of genera including *Caprimulgus* species. We found a clade of exclusively South American species including the genera *Caprimulgus*, *Uropsalis*, *Eleophthreptus* and *Hydropsalis*. We also found a clade of African and Eurasian nightjars including *Caprimulgus* and *Macrodipteryx*. Finally, we found a clade of North American birds containing just *Phalaenoptilus* and *Caprimulgus*. We also found that Australasian *Eurostopodus* was basal to all other caprimulgid genera sampled and has been supported by subsequent studies (Han *et al.* 2010, Sigurðsson and Cracraft 2014, White *et al.* 2016). Whether *Eurostopodus* or *Lyncornis* is the most basal species has still to be resolved (White *et al.* 2016). Two ecological factors appear to make morphological classification potentially misleading: first, the apparent retention of primitive anti-predator and foraging-related traits across genetically divergent groups; second, rapid divergence in other traits, especially those related to mating, which generate high levels of morphological divergence between species that are genetically very similar. The cytochrome *b* data suggests that the genus *Caprimulgus* is not monophyletic and is restricted to Africa and Eurasia and that *Caprimulgus* species from the New World have been misclassified as a consequence of retention of primitive adaptations for crepuscular/nocturnal living. Some other genera also appear to have little support from the cytochrome *b* data. “*Caprimulgus*” *longirostris*, *Caprimulgus* *cayennensis*, and *Eleothreptus* *candicans* were formerly placed in a separate genus, *Thermochalcis* (e.g., Cory 1918), but this was merged into *Caprimulgus* by Peters (1940). We found weak support that *longirostris* and *candicans* were closely related

(*cayennensis* not sampled) and propose that *longirostris* be renamed *Systellura* and *cayennensis* becomes *Hydropsalis* based upon the oldest first-named species (Cody 1918). The dense taxon sampling of New World nightjars in Sigurðsson & Cracrafts (2014) phylogeny, and a recent study by White *et al.* (2016) have expanded *Hydropsalis* to include *Systellura* and *Eleothreptus* and we agree with this proposal. We also found strong genetic support that *maculicaudus* was not a *Caprimulgus* but was a member of a group that includes *Hydropsalis*, *Uropsalis*, "*Caprimulgus*" *longirostris*, and *Eleothreptus candicans*. Barrowclough *et al.* (2006) largely agree with this although they didn't sample *candicans*. A sensible proposal would be to enlarge *Hydropsalis*, or at least include *maculicaudus* in *Hydropsalis*. Sigurðsson & Cracraft (2014) also placed *maculicaudus* in *Hydropsalis*.

7.1.1.v Chapter SIX

We used our phylogeny as the basis for exploring the distribution and function of facial bristles in the Caprimulgiformes, with detailed sampling within the Caprimulgidae. This is the first, phylogenetically controlled analysis of facial bristles in birds. Interspecific variation in rictal bristle number, length and stiffness is high in the nightjars, with functional bristles absent in the majority of the nighthawks (Chordeilinae) and considerable variation in the remaining two New World nightjar radiations and the Old World radiation. Our analyses showed that rictal bristle number and characteristics correlated with foraging habitat complexity, mouth area and foraging method, but less so with general habitat complexity. We suggest that rictal bristle number has a mechanical role in protecting delicate head structures from obstacles in general and foraging habitats. We also propose that complex foraging habitats select for longer, more flexible rictal bristles that have improved mechanoreception. It would appear from our results that nesting ecology has little effect on the presence of different bristles. Bristles are primitive and have become vestigial multiple times within this Order. These events are associated with habitat shifts leading to changes in foraging behaviour and selection on bristle

characteristics, which in turn may have led to speciation in these successful and enigmatic nocturnal birds.

7.1.2. Chapter Synthesis

The analysis of nightjar song territories and nests site characteristics in conjunction with measurement of nest success rates provides important understanding of habitat selection for predator avoidance in nightjars. Nightjars occurred in different habitats but spatial analysis at the territory scale showed that territories were consistently compact and nests were located adjacent to soft, rather than hard edges. At the scale of the nest, vegetative concealment varied with habitat with most nests located in vegetation of intermediate density to the range available. By combining this information with data on predation rate and nest survival strong evidence for predator mediated nest site selection and song territory shape emerges. Nests were predated at higher rates on clearfells in comparison to more established restock or traditional heathland habitat. Clearfell then has some of the hallmarks of an ecological trap (Battin 2004), and therefore clearfells should not be viewed as appropriate surrogates for more traditional nesting habitat. That said, if birds on young restocks locate their nests in optimally dense vegetation away from hard edges they will benefit in the long term from enhanced cover as the canopy closes. The relationship between territory size, shape and quality and relative predation is a complex one. For example, rapidly predated nests in large territories might be indicative of poor nest site choice by a poor quality male and not as evidence of the presence of high predator densities. Establishment of larger territories in sought after habitat might be important in reducing extra pair copulations.

Daily nest survival was explained by territory area and compactness ratio, edge type, and vegetation density. Surprisingly, nests in large territories were predated quickly and this suggests that the holders of such large territories defended them in response to the perceived threat of predation (Fontaine and Martin 2006). This sense or ‘fearscape’ might be an important determinant in habitat selection (Olsoy *et al.* 2015) and should be

considered in future studies. Nightjar (and artificial) nests in compact territories survived longer than those in less compact territories so it seems that birds can compensate for the threat of predation by defending 'circular' territories and locating the nest away from hard edges. However, the importance of nest concealment should not be underestimated, as nests survived for longer in dense vegetation. Knowledge that controlled nest visitation did not negatively affect nest success, regardless of nest location, is reassuring and should be noted by future researchers and habitat managers. Furthermore, for such reclusive species with low nesting density artificial nests provide useful baseline information about predation patterns and possible explanations for habitat selection.

The publication of the molecular phylogeny of the nightjars presented in Chapter Five provides an opportunity for comparative studies on behaviour or morphology and the analysis in Chapter Six would not have been possible without it. The opportunity to map characters onto a well-resolved, albeit composite phylogeny, makes questions about causes of change in form and function answerable. We have already measured other traits, besides bristles, and the results are promising.

7.1.3. General methods

This is the first study to review the effects of the research techniques on nightjars. In keeping with previous work on habitat use by nightjars we used telemetry (e.g., Alexander and Cresswell 1990 and Cross *et al.* 2005). Once again, this proved to be a useful way of locating a stationary bird in the dark for the purpose of song territory analysis but was less effective for determining a bird's location when it was flying due to problems in acquiring an adequate number of fixes (Cross *et al.* 2005). This was the first time backpack harness transmitters were used on nightjars and these proved to be useful for determining types of activity.

Using both territory mapping and MCPs generated from telemetric data were effective ways to census the nightjar populations revealing that birds shared airspace within

neighbouring territories. We could have analysed the habitat used for song territories versus the habitat available to the birds in the forests (as both sets of data are provided) but that was not the focus of this study. There are issues with generating measures of 'available' habitat, e.g., the sum of a particular habitat type within a specified area but without an understanding of the ecology of a species such an approach is naive. Availability should include both the accessibility and procurability of habitat, not just their abundance (Martin 1998, Jones 2001 provides an excellent review). For example, nightjars have been shown not to nest in suitable habitat when the diameter of the habitat is less than 50m (Wichmann 2004) or if that habitat is adjacent to housing (Liley and Clarke 2003) or footpaths (Murison 2002, Langston *et al.* 2007). Including such habitat in estimates of 'available' habitat would lead to overestimates and therein apparent avoidance. We tested habitat selectivity by comparing nightjar nests/territories with randomly stratified ones and this proved to be an effective and sensitive method for determining habitat choice in this species.

The choice of artificial nests to replicate predation of nightjars nests was, on reflection, useful for identifying the importance of nest site selection on predation rate and nest survival but less so for identifying predator assemblage. For future studies, we recommend the use of small nest cameras with infrared sensors for identifying predation events, but at the time of this fieldwork such technology was not affordable (e.g., Benson, Brown and Bednarz 2010). Such camera footage could be used in conjunction with the backpack harness tags to help calibrate the signal from the thermistor with the activity of the bird to provide additional information about parental care at the nest.

Taking blood samples (for DNA extraction) may have had long term effects on adult nightjars and their chicks and should be avoided. Instead, contour feathers can be collected from birds and DNA is extracted from the tips.

Cytochrome *b* proved to be a useful probe of Caprimulgidae systematics but this varied with the depth of the node. At the species and subspecies level it was very effective at resolving relationships providing high bootstrap support for nodes and conclusive evidence that Caprimulgus is not monophyletic. However, it was less effective at resolving relationships at deeper nodes and could not provide supportable hypotheses for the evolutionary order of the main biogeographical clades or the branching of the other Caprimulgiform families. The inability of cytochrome *b* to resolve these relationships might be down to the rapid radiation of this group followed by saturation of the rapidly mutating cytochrome *b* gene over the long evolutionary time period this group appear to have existed.

The Bayesian analysis used in the study overcomes some of the problems associated with traditional methods such as parsimony and maximum likelihood (that we also used) because it accounts for phylogenetic uncertainty (Huelsenbeck and Ronquist 2001). It uses prior information about probabilities (posterior probabilities), updating them as new information becomes available and incorporates more complex models of evolution.

By choosing to use a comparative approach for testing hypotheses about facial bristle function and evolutionary distribution, on a well-resolved phylogeny, it allowed us to arrive at key conclusions. Many studies in the past have not used such robust phylogenetically controlled analysis and therefore their conclusions are unsubstantiated (Grafen 1989, McKechnie, Freckleton and Jetz, 2006). The choice of outgroup(s) was problematic because the Order was paraphyletic when the analysis was completed (e.g., Mayr 2010, Jetz et 2012) but when analyses were run with different ordering or numbers of outgroup species the results were not significantly different. However, we provide a detailed comparative dataset that should be useful for subsequent studies on this group.

7.1.4. Future research

7.1.4.i Conservation ecology work

This thesis has provided opportunities for a number of further investigations and these in turn might benefit the findings of this thesis. The song territory analysis revealed two surprising results; mated and unmated males had song territories of a similar size and territories of neighbouring males often overlapped. This raises questions about the accuracy of nightjar censuses based upon territory mapping. The frequency of territory overlap and of song post sharing could be factored into subsequent population censuses to arrive at a more accurate estimate. One could repeatedly randomly sample the song posts of neighbouring males from the existing data set and arrive at an estimate of the probability of the fieldworker counting those birds in one territory for any given night's census. Knowledge about song characteristics and behaviour of mated and unmated males could also be factored into the training of census workers to help improve the accuracy of breeding censuses.

A radio tagged unmated male who frequently sang from within a paired male's territory was observed helping feed the young of the first brood. The results of a parentage analysis (not presented here) using multilocus fingerprinting revealed he was not related to the chicks nor the adults. Helping rear the young of other males might be a consequence of the skewed sex ratio in these populations but might also be the product of females actively switching males for the second brood (Cresswell and Alexander 1990). The combination of radio telemetry and DNA fingerprinting would help to unravel the phenomena of 'nest helpers' and mate switching in this species.

Methodological and technological improvements now provide ecologists with the ability to measure the psychological (Clinchy *et al.* 2013) and physiological (Zanette *et al.* 2014) responses of prey to predation threat (including human) and these have led to the development of a more general framework for understanding nest predation. Although the research methods used in this thesis were found to have no measurable long term

effect on adult nightjars, bleeding reduced the rate of weight gain in chicks. An interesting experiment would be to see whether the psychology of males had changed in response to being instrumented or bled, resulting in an increase in their territory size the following year? The concept of a 'fearscape' has been increasingly applied to habitat selection by animals (Olsoy *et al.* 2015) and the perceived threat of predation might have significant effects on habitat selection in prey species. An experimental removal of predators might result in a paralleled change in habitat selection by prey and this would provide a better understanding about habitat use versus availability.

Research suggests that birds increase their territory size when perceived threat of predation increases so one would predict that males that had experienced significant disturbance would respond in a similar manner (Adams 2001). Furthermore, knowledge on site fidelity in females as adults is lacking. Females might be more likely to return to breed with the same male if they were successful the previous year (Piper 2012). However, if a breeding female is fitted with a transmitter or bled does she return to same male's territory or disperse? If the latter, this might have long term effects on the viability of small isolated populations of nightjars. Physiological responses to handling and blood loss might have compounding effects on stress levels (Romero and Romero 2002). One could measure corticosterone levels in netted but not bled birds versus netted and bled birds. Certainly, psychological and physiological responses of prey to perceived threats appear to be fruitful areas of investigation.

Blood sampling on the scale reported here had no measurable long term effects on adult nightjar. This should reassure researchers who aim to conduct work that requires blood sample collection - e.g., mating system analysis or population work but researchers should endeavour to design experiments on animals that involve the fewest effects (Festing *et al.* 2002) and consider using alternative for DNA analysis.

We found evidence that the proximity of foraging habitat affected nightjar song territory size (Brown 1964) and territory occupancy (Bowden and Green 1990) and this has recently been supported by Sharps (2013) and for other avian species - e.g., kingfishers (Kesler 2012). Analysis of home range and song territories in relation to foraging habitat would therefore be a profitable area of investigation. Accurate home ranges can be difficult to generate for this species (e.g., Cross *et al.* 2005 but see Sharps *et al.* 2015). In order to determine a more accurate measure of home range one could use satellite transmitters and this has become an increasingly popular method (Hooijmeijer *et al.* 2013). Not only would these provide a greater number of fixes for the analysis of home range but could be used to monitor migration routes and wintering grounds of nightjars which has received only superficial treatment (Cresswell and Edwards 2013).

This study only looked at the importance of habitat selection for nest sites and predation during the incubation period and additional information could be gathered from the brooding period. Other research has shown that nest crypsis is less important during the brooding stage (e.g., Remes 2005) but there are likely to be more natural cues available to predators once eggs have hatched (Burhans and Thompson 1998). The brooding period is a similar length to the incubation period and parental activity increases so opportunities for predation are likely to be high. Vegetative concealment is also likely to have increased at this stage in the nesting cycle and this might to be an important variable in nest survival. Our results suggest that predators did not respond equally to nightjar and artificial nests containing plasticine eggs. As these were deployed to identify nest predators an alternative for future studies would be the use of small nest cameras.

It was reassuring to find that researcher activity did not have a measurable effect on nightjar nest success. This study only measured disturbance in terms of 'visited' and 'unvisited' nests but the frequency, i.e. a one off visit compared to daily, weekly etc. visits was not measured. Rate of visitation has been shown to be important in nest predation with frequently visited nests incurring more predation than infrequently visited nests

(Reynolds and Schoech 2012). The rates at which we visited nightjar nests might have been below the threshold required to initiate a predatory response but to attempt to achieve this (i.e. a high enough intensity of visits) on a nightjar population would not be advisable. Artificial nests using quail eggs would be ideal to test this. Future studies using artificial nests should aim to follow the advice provided by Major and Kendal (1996) who concluded that future experiments be required to include; (i) a *natural control*, i.e. real nests of the species under study, monitored and treated in the same way as the artificial control; (ii) an *artificial control*, i.e. artificial nests differing from the natural nest only on account of being artificial, but differing from the artificial treatment solely by the variable under observation; (iii) the *artificial treatment*, i.e. artificial nests constructed to examine the effect of a single variable. By only focussing on one variable, i.e. ‘nest visit’ versus ‘no nest visit’, and by including natural and artificial controls, and an artificial treatment, this study was able to find no evidence for increased predation caused by nest visitation. Indeed, in one habitat type there was a positive effect of nest disturbance on artificial nest success and we put this down to predators avoiding humans.

Predation is clearly a critical factor in nests success but most studies on habitat selection in birds focus on how prey avoid predation and less so on how predators search for prey (Ibanez-Alamo *et al.* 2015). New ecological perspectives and understanding of how predators search (Pelech *et al.* 2010), will help fieldworkers design more sophisticated experiments for measuring habitat selection. The attachment of GPS tags to predators of nightjars would provide accurate data on home range size and habitat use and provide habitat managers with key information about the likelihood of nest predation. This might inform conservation initiatives about acceptable levels of nest disturbance due to habitat management or researcher activity which are particularly important in commercial pine plantations where routine crop maintenance takes place and where recreational disturbance is likely.

7.1.4.ii. Phylogenetic and comparative work

This nightjar phylogeny achieved its aim of testing the Monophyly of the genus *Caprimulgus* but could not resolve branching deeper within the family despite observations by Moore and DeFilippis (1997) that cytochrome *b* is very effective at resolving relationships at the family to subspecies level. A phylogeny based upon a less rapidly evolving nuclear gene would therefore be more informative, as has been shown to be the case (Han *et al.* 2010, Sigurðsson and Cracraft 2014). Furthermore increased sequence and increased taxa would also help to resolve relationships. Sigurðsson and Cracraft (2014) have produced by far the most comprehensive phylogeny on this group, largely supporting the four biogeographic clades we identified. Any future work needs to include Old World taxa and in particular monotypic genera such as *Veles binotatus* and more species of eared-nightjar to establish the basal ordering of *Lyncornis* and *Eurostopodus* (White *et al.* 2016).

Comparative studies are only as good as the phylogenies upon which they are based and for nightjars these are good (e.g., Han *et al.* 2010, Sigurðsson and Cracraft 2014, White *et al.* 2016). Our conclusions about the importance of bristles in the speciation of the nightjars would be enhanced by a detailed ancestral state reconstruction and procedures and software to do this are well established. The bristle work would benefit greatly from knowledge on bristle histology and in particular presence of Herbst corpuscles or muscles for innervation. Initial enquiries show that spirit samples for many Caprimulgiformes exist in UK museum bird collections and I have been granted permission for destructive sampling by the Natural History Museum, Tring. The author is currently writing a manuscript on bristle function and distribution in Aves and analysis of museum specimens and the literature suggests that facial bristles occur in ~80 bird families with diverse ecologies and evolutionary histories. New phylogenies that have resolved much of the paraphyly amongst avian lineages (e.g., Jarvis *et al.* 2014), provide phylogenetic frameworks for testing the evolution and function of such common morphological traits

and suggest that subsequent analyses of this group include the Apodiformes (Prum *et al.* 2015).

Other comparative work is still to be done. We have already conducted an analysis of plumage white patches in the Caprimulgidae, extending the work done by Pople (2003), and these results are very promising. In keeping with our work on foraging adaptations it would be interesting to perform a comparative study of stomach anatomy and capacity of Caprimulgiformes in relation to their foraging ecology. Due to restrictions imposed by their bimodal foraging activity periods at dusk and dawn there is a likelihood that they have to 'cram' their stomachs during these limited feeding opportunities.

There is still so much not known about this difficult to study group with many general aspects of foraging and nesting ecology undescribed for many species. However, as with many bird families with low reproductive rates they may be particularly vulnerable to extinction (Bennett and Owens, 1997). Therefore, there are many opportunities for future work to have a considerable impact in enhancing our knowledge of their conservation ecology and ensure the futures of these enigmatic night birds.

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